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ABSTRACT

This is one of several study guides on contemporary problems produced by the American Association for the Advancement of Science with support of the National Science Foundation. This document was a working draft on the topic for the lectures. Included are sections on the following topics: (1) Biosociology and Behavior; (2) The Social Bond; (3) Structures of Social Groups; (4) Communication; (5) References; (6) Instructional Materials; and (7) Student Projects and Exercises. (RH)

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AAAS STUDY GUIDES ON CONTEMPORARY PROBLEMS

Since 1970 the American Association for the Advancement of Science has conducted the NSF Chautauqua-Type Short Courses for College Teachers Program with the support of the Education Directorate of the National Science Foundation. More than 9,000 college teachers of undergraduate students have participated in the courses which have dealt with either broad interdisciplinary problems of science or the applications of science and mathematics to college teaching. All of the courses are designed to make available the most current information.

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The second series of six Study Guides based on courses in the 1975-76 program will be tested during the coming academic year. After testing and revision, the following titles should be available from AAAS in the late fall of 1976:

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* * *

This Study Guide was prepared in rough form in late 1974 - early 1975, with full intentions to thoroughly revise it after a trial run in one of the Chatauqua Lecture Circuits and after critical reviews by a number of colleagues. Some sections, most notably materials relating to the evolution of sociality and social bonds, were virtually ignored in the present manuscript since these topics were in major ferment during 1975; the revision, which was planned for 1976, was to take into account the latest ideas and arguments. At the same time, unnecessary materials were to be weeded out, references and citations were to be checked, and sections that were unclear or misleading were to be rewritten.

The revision was not accomplished, so that what is here is in fact a raw working manuscript, unreviewed, uncritiqued and admittedly uneven. The reader who is interested in modern concepts of biosociology (and perhaps sociobiology) is advised to skim these pages very rapidly for traditional background material and then go elsewhere for more up-to-date ideas and arguments.

Martin W. Schein

* * *

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PREFACE FROM AAAS

TO STUDY GUIDE REVIEWERS:

The test editions of the set of six Study Guides were prepared on relatively short notice by the course directors during the summer of 1975. To provide as much information as possible to the authors for use in revising this study guide for publication, we ask you as a participant in the NSF Chautauqua-Type Short Course to test these materials and provide your reactions. Also we would appreciate receiving reactions of your colleagues and students if that is possible. Your efforts will contribute significantly to the quality of the revised Study Guide.

If this Study Guide has been successfully prepared, upon completing it, you will: (i) have an overall comprehension of the scope of the problem, (ii) understand the relationships between aspects of the problem and their implications for human welfare, and (iii) possess a reliable guide for studying one or more aspects of the problem in greater depth. We ask you to evaluate the study guide on the basis of how well each of these objectives is achieved. Of less importance but most welcome are your specific editorial suggestions, including punctuation, syntax, vocabulary, accuracy of references, effectiveness of illustrations, usefulness and organization of tabular materials, and other aspects of the draft that are related to its function. Three copies of an evaluation form follow this page and additional copies may be reproduced if needed. Each evaluator should return a completed form to: NSF Chautauqua-Type Short Course Program, AAAS, 1776 Massachusetts Avenue, N.W., Washington, D.C. 20036. Please type or print legibly. Feel free to include any additional comments you care to make. This evaluation is in addition to any evaluative requests made by the study guide authors; however, we do encourage you to cooperate with all requests from authors. Your efforts in evaluating this Study Guide are a worthwhile contribution to the improvement of undergraduate education and we express our appreciation to you.

We hereby gratefully acknowledge the services of Joan G. Creager, Consulting Editor, and Orin McCarley, Production Manager for this series.

Arthur H. Livermore
Acting Director of Education
AAAS

Don I. Phillips
Project Director

AAAS EVALUATION FORM

After completing this study guide, tear out one copy of this sheet, complete it, fold, and mail. No envelope is needed.
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Author's Preface

This manuscript should be considered as a working draft and treated almost as a privileged communication. Because of pressures imposed by short notice and a very tight deadline, there has not been time to thoroughly check out all the references, to gather in all the associated materials, nor even to pursue completely the ramifications of some of the ideas raised. Perhaps more importantly, there has not been time to follow the usual procedure of sending the manuscript out for preliminary critical review.

You therefore have before you a very raw working draft, with all the faults and shortcomings that are implied by an early stage of development. This means that you, the reader, are cast into the role of a critical reviewer and I would certainly appreciate and welcome your general and detailed comments above and beyond the evaluation forms that are included in the guide. The deadline for the final draft is the summer of 1976, so there's now plenty of time to give the present draft a thorough working over.

M. W. Schein
Morgantown, W. Va.
August, 1975

BIOSOCIOLOGY

Biosociology, the study of the biological bases of social interactions and social organization, is a relatively new field that has important implications to the conduct of human affairs. It is a natural outgrowth of behavioral ecology studies, but its roots draw from many seemingly diverse areas: on the phylogenetic spectrum, we may list the fields of protozoology, entomology, ichthyology, herpetology, ornithology, mammalogy, primatology and anthropology; on another axis we may list such areas as genetics, physiology, development, ecology, ethology, zoosemiotics, psychology and sociology; on a still broader (and perhaps all encompassing axis), we may list organismal, populational, and evolutionary biology.

My own approach to Biosociology is through its animal behavior/ethology roots. Hence, some overall familiarity with the field of behavior, its concepts, techniques, and jargon is necessary at the outset in order to understand more fully the development of the social behavior theme. However, I will not hesitate to draw freely upon inputs and contributions from other discipline areas as needs arise and as occasions warrant.

I. BIOSOCIOLOGY AND BEHAVIOR

Animal Behavior

Animal behavior as a field of study is concerned with the motor activities of an intact organism as it interacts with the environment. A behaviorist is interested in the internal mechanisms that cause the

motor activities to occur, in the external factors that bring the internal mechanisms into play, and in the consequences of the motor activities.

The word "behavior" is used to broadly denote the sum total of the animal's motor activities ("the mouse's behavior in a strange environment") and is also used to denote a specific activity pattern of the animal ("the mouse's feeding behavior"). Thus, the overall "behavior" of the animal is best described as a complex interaction of a number of specific "behaviors". This dual interpretation of the term usually does not lead to confusion and misunderstanding so long as the context of usage is clear, but the reader must be aware of the possible semantic difficulties.

Behavior is a motor activity. The unit of behavior is the pattern, an organized segment of activity that is consistent and normally fulfills a special function. This is "what an animal does". It is organized in that it is non-random, and consistent in that the particular sequence of muscular movements is observed repeatedly. It fulfills a special function in that patterns are adaptive, i.e., they contribute to the survival of the individual or to the survival of the species. Some patterns (e.g., taking in food or avoiding a threatening stimulus) have more immediate and obvious survival values than others (e.g., examining a new object in the environment or play-fighting among young), but all are adaptive or at least not maladaptive. Maladaptive behaviors perish with the organism and so are not transmitted to future generations.

A behavior pattern does not occur in a vacuum; something causes it to occur and this cause is called a behavioral stimulus. The stimulus is information that the organism assembles by way of its various sensory

modalities, interprets in its nervous system, and then reacts to. Much information, from both internal and external sources, impinge on the organism at all times, but the major proportion (probably over 99%) is ignored as being insignificant and unimportant at the moment. Only that information that results in a motor action can properly be termed a behavioral stimulus. This of course means that some object or movement may serve as a stimulus on one occasion and not on another. We shall have more to say about this later.

The link between the triggering stimulus and the pattern it elicits is often intriguingly complex and usually involves a fair proportion of the organism's physiological mechanisms. Mechanisms of behavior include the workings and interrelationships among perceptual, neural, endocrinological, and locomotor systems and all the attendent physical, mechanical, and chemical systems and structures upon which they are based. Whether or not a stimulus elicits a pattern often depends upon the animal's physiological state at the moment: a sexual signal does not elicit sexual behavior from a turkey outside of the breeding season, i.e., when it is physiologically unprepared to act upon the signal; the same signal during breeding season could set into motion a series of discrete mechanisms and acts leading to a successful mating.

Given a defineable stimulus that triggers an observable motor pattern, further analysis demands quantification. A one-to-one relationship between the stimulus and its elicited pattern would automatically determine the level or quantity of behavior: the more stimulus the more behavior. But such one-to-one relationships are rare; more commonly, the stimulus has to reach some threshold of intensity before any of the pattern is triggered, and thereafter a unit increase in stimulus results in some

proportion (including the possibility of zero) of a unit increase in exhibited pattern. For example, in eliminative behavior the act of defecation is triggered by internal signals from the animal's gut. The signals must reach some level of intensity before the animal begins to react, and in some secretive species the reaction involves a complex series of activities. Doubling the quantity of excrement to be passed does not necessarily result in doubling the intensity or quantity of time involved in digging a hole or covering the feces or any of the many acts performed by the various species.

Finally, given an observable pattern and knowledge of 1) its eliciting stimulus, 2) the mechanistic link between the stimulus and the pattern, and 3) a measure of the levels of behavior exhibited, we need further to know the consequences of performing that particular act. Short-term consequence questions such as the effects of the act on nearby neighbors are immediately pertinent to this study guide. Long-term consequence questions, such as survival of the act and increased fitness, are perhaps more peripheral to our immediate needs but are no less important for the study of behavior and biosociology.

The five parameters, patterns, stimuli, mechanisms, levels, and consequences constitute the what, why, how, how much, and so what of behavior. They are critically important to analyses (and therefore understanding) of behavior. They are interdependent, but they may be independently studied by the usual expedient of holding any one constant, varying another and recording the resulting variation in a third. While this dictum seems perfectly obvious, it cannot be overemphasized. Confusion as to which parameter is under study could lead to serious erroneous conclusions.

Selection of appropriate indices to use in quantifying behavior demands a thorough understanding of the stimulus situation and the pattern being studied. Inappropriate stimuli often lead to distorted patterns which in turn lead to erroneous measures of levels. Further, a level of "zero" could reflect either the animal's constitutional inability to perform a certain action or simply an improper stimulus situation; it remains to the investigator, and indeed is a responsibility, to discover which is the case.

Consider, for example, an interesting study of the sexual performance of dairy bulls at an Artificial Insemination Center. Naive, young, normal bulls, when confronted with their first sexual situation, respond within minutes and have little difficulty in reaching ejaculation. On the other hand, naive blind bulls who are otherwise healthy, or intact naive bulls that are blindfolded, are sluggish performers: put into their first sexual situation, they often require many hours before mounting the stimulus animal and ejaculating, if indeed they ever mount. Confronted with these observations, one might conclude that the level of sexual performance of blind or blindfolded bulls is orders of magnitude lower than their visually intact brothers, levels in this case being measured either as the number of ejaculates per unit time or the quantity of time required to achieve ejaculation.

Pursuing the investigation a bit further, however, it was discovered that while the second ejaculate of the visually intact animal was achieved some five to ten times quicker than the first, the second ejaculate of blind bulls was reached hundreds of times more rapidly than the first; indeed, performances of the blind bulls on second ejaculates were quite comparable to those of the intact animals. The investigators had to

conclude that the apparent deficit in sexual behavior of blind (or blindfolded) bulls was merely a reflection of the animal's inability to recognize a sexual situation. Once this information was gained by the animal, he performed as well as if he had the use of his eyes. Thus, there was no difference in levels of sexual behavior when the stimulus situation was adjusted to the sensory capabilities of the different animals.

The student of behavior treads a delicate semantic path between the quagmire of teleology on the one side and the quicksand of anthropormophism on the other. In a teleological approach, the function of the pattern is confused with its cause: the animal eats "in order to" survive and mates because the "purpose" of mating is to perpetuate the species; some rational awareness of the distant future is often implied. In an anthropormorphic approach, the animal is endowed with human sensitivities and capabilities, and responds to situations just as you or I might do: the animal eats "because it is hungry" (meaning that when you and I have not eaten for several hours, we get hungry and therefore eat) and it mates "because the act is gratifying" (meaning that we consider it pleasurable).

Either of these approaches can lead to difficulties in analyses of behavior. Ascribing causes to functions leads to a dead end and obfuscates the objective search for mechanistic causes that help us understand, if not explain, the behavior in question. When we ask "why" such and such a behavior occurs, we do not mean "What is its purpose?" but rather "What are the mechanisms leading to its occurrance and what are the consequences?" In other words, the observed behavior is the effect of some causes and the cause of some effects as yet to be determined. The observable end effect, the final consequence, is neither an end nor final since in itself it is another cause; still, it is a convenient stopping

place for us, since now we think we can recognize the use to which the chain of events leading to this point may be put: the function. Thus, function is merely a semantic device, a label, that we attach to a chain of events; if anything, it occurs after the fact and in no way can be interpreted as the cause, mechanism, initiator, or generator of the activity.

The anthropomorphic approach elicits no serious attack, for in the absence of evidence to the contrary, we simply cannot ascribe human sensitivities to non-human forms. Does the fly "like" sugar solutions in the way that some of us "like" ice cream? In both cases, preferences are demonstrable, but is the "liking", the sensual gratification, the same? Does the chicken avoid a particular flockmate because it "knows" that the consequences of a meeting would be disastrous, in the same way we often avoid a bully because we "know" that a confrontation would be unpleasant? Again, the active avoidance in both cases can be demonstrated objectively, but is the "knowing", the awareness of the consequences, the same? We cannot answer these questions as yet and indeed may never be able to do so. Therefore, it is much safer to exercise caution, not to consider chickens as little men with wings and feathers nor flies as little men with enormous eyes and a built-in buzzing system. No, let the observer gain the experience, skill and talent to cast himself in the role of a chicken without feathers or a fly with small eyes, and he might then be a better student of behavior.

Patterns of Behavior

Behavior patterns are easily described, but not so easily categorized, partly because the function fulfilled by the pattern is not always obvious to the observer. Still, there is enough consistency in some clusters of activities to permit us to classify behaviors into various groupings and assign labels for the categories. This, then, is the language of behavior. Each classification encompasses many movements, many particulate acts, and a number of such movements serve multiple functions and therefore appear in several classifications. Because of this, the reader must bear in mind that these categories are at best loose descriptions that permit us, the audience, to discuss what is happening; they are in no way binding upon the actors themselves.

The following categorization is based in part upon Scott's (1958) original list of nine general types of adaptive behavior. I have taken the liberty of expanding Scott's list to twelve general groupings, and in some cases I have chosen to deviate from Scott's original labels. Further, I have separated out those behaviors that an animal normally does (or can or will do) alone (the individual behaviors) from those behaviors that normally demand interaction with at least one other individual (the social behaviors). The word "normally" is to be taken in its broadest sense; I fully realize that individuals, populations and even whole species can deviate from the norm.

The Individual Behaviors

1. Ingestive Behavior. This label incorporates all activities related to the taking in of nourishing substances, either solid or liquid. It is a somewhat broader term than the more limited concepts of "eating",

"drinking" or "feeding", which often appear in the literature in more specific contexts. Patterns of ingestive behavior are closely determined by the nature of the characteristic foods of various species, which in turn are related to the anatomical and physiological attributes of the species. Thus the ingestive patterns exhibited by seed-eating birds are quite different from those exhibited by scavenger birds, and the sucking insects differ markedly from biting insects in their approaches to food. The nature of the ingestive complex often has profound effects on the structures of social groups or the geographical niches occupied by the species. I need only the mention the lion, a carnivore, and the antelope, an herbivore, to make the point obvious. While ingestive behavior is frequently exhibited in a social context, especially in some species, I consider it an individual behavior in that the animal will normally exhibit this behavior even if removed from its social milieu.

2. Eliminative Behavior. All activities related to the elimination of waste products are classified under eliminative behavior. The patterns are relatively uncomplicated in most species and purely the acts of individuals without regard to the presence or absence of others. However, it must be recognized that in some species, eliminative patterns are quite elaborate (e.g., burial of feces) and still others use waste products (e.g., urine markings) to convey specific information to others in a highly social context. Nevertheless, in most species, eliminative patterns are clearly within the realm of individual behaviors.

3. Shelter-seeking Behavior. This broad category of behavior encompasses all activities that the animal undertakes in an effort to achieve environmental homeostasis. Activities such as burrowing, nesting, getting in out of the rain, or somehow or other moving into or creating a

more optimum physical environment would fall into this category. Under some conditions, shelter-seeking behavior is a highly social activity (e.g., the nest constructed by a mated pair of birds) and indeed communal activity may be typical for the species. Nevertheless, in many or most animal species, shelter-seeking is generally an individual activity.

4. Investigatory Behavior. This category includes any behaviors that result in familiarization with the immediate environment. It is especially apparent when an animal has moved into a new situation, but is still exhibited to some extent by animals in old, familiar surroundings. While investigatory behavior and the consequent familiarization with the terrain is important to the survival of the individual, it is usually a "low priority" behavior that is expressed only when more immediate needs are met or when more immediate threats are diminished. In many species, levels of expression of investigatory behavior are inversely related to age, probably because the older individual is more likely to be well established in its terrain and therefore less likely to confront new environmental situations.

5. Sleep Behavior. As with other 'individual' patterns, behavioral sleep often appears in a social context. Nevertheless, I still include it among the individual behaviors because an isolated individual can and will sleep: there is no need for multi-animal interactions in order for sleep to be expressed. Species-typical sleep patterns vary markedly: postures in terrestrial forms range from hanging to standing to sitting to lying prone or curled, and temporal patterns range from many short "catnaps" to long periods of uninterrupted slumber. Depth of sleep also varies from barely somnulent to deep torpor, and there is still a question as to how extensive sleep really is across the phylogenetic spectrum.

It is well to bear in mind that behavioral sleep and physiological sleep might be quite different: individuals exhibiting all the behavioral signs of being asleep might in fact be physiologically quite alert (as demonstrated by EEG patterns and other physiological measures), and the converse is probably also true.

6. Anti-Predator Behavior. This category of behavior, which includes all acts performed in response to an immediate threat to the life of the individual, has not received much attention until recently primarily because little or no distinction was made between defense from predators and defense from conspecifics (see Agonistic Behavior, below). However, I wish here to make that distinction clear chiefly on the grounds that loss of an encounter with a predator usually means death while loss of an encounter with a conspecific rarely leads to death. It is my impression that in interspecific defense, behavioral patterns differ (markedly in some cases, subtly in other cases) from those exhibited in intraspecific defense. Skunks and rattlesnakes use their very effective deterrent weapons in interspecific, rather than intraspecific interactions. In those instances and species where conspecific interactions often lead to the death of the loser, then the intraspecific defense behavior patterns merge into anti-predator behavior patterns. While anti-predator behaviors involve cooperative efforts of conspecifics in some species (mobbing in some species of birds, the defensive ring of musk oxen, are good examples), for the most part the behavior is primarily the responsibility of the individual.

7. Play Behavior. In spite of recent efforts no understand the the physiological and behavioral relevance of play, it still remains as a largely ununderstood category of behavior except perhaps in humans. It

may surprise some readers that I choose to list play behavior as an individual rather than as a social behavior, but I do so on the grounds that play can be and is exhibited by individuals that do not have the benefit of company. Of course, if receptive individuals are around, then play takes on decidedly social forms. By and large, the levels of play behavior are (like investigatory behavior) inversely related to age. How far play extends across the phylogenetic spectrum, or whether it appears at all in invertebrates and lower vertebrates, is still an open question. While play behavior is listed as an individual activity, it probably has very important social implications in at least some species.

The Social Behaviors

8. Sexual Behavior. Associated with each species is a characteristic series of activities clustered under the rubric, 'sexual behavior'. Pre-copulatory (courtship), copulatory and post-copulatory behaviors are all included in sexual behavior. The patterns are usually quite elaborate, and since at least two individuals are involved, intricate signal systems have been developed. Not only are the patterns specific to a species, but within species they are specific to a sex: the sexual patterns characteristic of male chimpanzees are different from those of female chimpanzees; together, they constitute the species-specific sexual pattern of chimpanzees.

9. Parental Behavior. Parental behavior (also termed "epimeletic" behavior by some workers) includes all those activities associated with the care of the young. Such diverse activities as nursing, nest building, brooding, cleaning and grooming, feeding, and defending the young are all part of parental behavior. Depending upon the species, parental

behavior may be exhibited by the mother only, the father only, both the mother and the father, or neither the mother nor the father. In the latter case,the species may lack any demonstrable repertoire of parental activities (as in flies and many other invertebrates) or parental duties may normally be assumed by individuals other than the parents (as in honeybees).

10. Care-Soliciting Behavior. Termed et-epimeletic behavior by Scott (1958) (in contrast to care-giving or epimeletic behavior, which I have chosen to call parental behavior), care-soliciting behavior describes those actions on the part of one animal that lead to attention or care provided by another. It is frequently considered as the other end of parental behavior: here, the young solicits attention from its parent. However, in addition to interactions with parents, care-soliciting behavior can also be observed among less closely related individuals and in older animals as well. Presenting for grooming in adult primates is probably akin to care-soliciting behavior, and elements of care-soliciting behavior appear in courtship routines in many species.

11. Agonistic Behavior. Just as each species has its own species-typical patterns of sexual behaviors, so does it have quite specific, often stereotyped, patterns of agonistic behaviors. A major difference might be that agonistic behavior patterns are rarely sex-specific. Agonistic behaviors encompass all acts related to competitive interactions between individuals; the intensity of agonistic behaviors ranges from simple (and often subtle) threats to overt challenges to outright physical combat and its resolution. Since agonistic behaviors are based upon competition for one resource or another, resolution of the conflict usually means that one

member gains the resource (i.e., "wins") while the other relinquishes the resource (i.e., "loses") at least for the moment. Agonistic behaviors are two-sided: on the winning side, threats, attacks, fights, chases and the like are observed; on the losing side avoidances, submissions, retreats, defenses and flights are observed. The term "aggression" is reserved to denote only which individual initiates the encounter, if such can be determined. Thus, the animal that attacks another is exhibiting aggressive behavior; the attackee will respond accordingly, probably by fight or flight behavior. Both are exhibiting agonistic behavior, but only one is aggressing.

It might be appropriate to insert here a few comments on agonistic behavior. First, while the initiator of an interaction, the aggressor, may have something of a momentary advantage, it is not a sine qua non that it will necessarily emerge the victor. The story of the bully who backs down when his challenge is met head-on has many counterparts in the non-human world. Second, agonistic interactions are usually resolved when one member relinquishes the sought-after resource; the relinquisher can then go about its business and adjust to the new, if somewhat unhappy, state of affairs. Indeed, if the resource is exceptionally important, it might very well attempt to gain it from another individual. Such a resolution is significantly different from the price of "losing" to a predator, where the life of the individual is the sought-after resource. It is on this basis that I separate defensive behaviors in agonistic behavior from those exhibited in anti-predator behavior.

12. Facilitative Behavior. Scott uses the term allelomimetic behavior to describe the situation where two or more animals "do the same

thing" and some degree of mutual stimulation can be demonstrated. I prefer a somewhat broader term, facilitative behavior, to encompass not only the mimetic aspect but in addition those situations where not necessarily the same behavior is expressed as a result of stimulation from another. The term facilitative behavior also includes behaviors that are intensified (i.e., higher levels expressed) as a result of inter-individual stimulation. Guhl (1965) describes a situation that has since become classic: the chicken that has just eaten its fill will quickly return to the trough to eat when confronted with a hungry neighbor that suddenly is allowed access to food.

Social Behavior

It is time now to look at social behavior and sociality from a much broader perspective than that used above. Previously, I had separated social behaviors from individual behaviors on the simple basis of the number of individuals required to carry the act to a successful conclusion. But there are at least some events (possibly many) involving more than one individual that we would not necessarily term "social". Consider, for example, a predator-prey interaction between a cat and a mouse; it could hardly be termed a social event in any sense of the word. In fact, the cat is clearly engaged in some aspect of its ingestive behavior patterns, while the mouse is ready to call into play all the anti-predator strategies at its command. Thus, the criterion of "two or more individuals" is clearly not sufficient unto itself to define sociality. What other criteria do we need to postulate? In order to answer this question, we need to look further at some characteristics that are invariably associated

with social groups and then examine the characteristics to see how invariant they really are.

Organization in Space

Let us postulate for the moment an hypothetical environment that is boundless (i.e., sufficiently large for whatever species we wish to observe) and where the resources are evenly distributed throughout the space. Let us then release into the space some finite number of individuals, say 50 or 100, all of them members of the same species. If we were to observe this group some period of time later, or even observe them continuously over time, we would find that with respect to the arrangement of individuals in space, only one of two conditions can emerge: they will either be randomly or non-randomly dispersed throughout the space. If they are generally randomly dispersed (with perhaps only occasional mating interactions to violate the randomness), then we could conclude that the individuals of this particular species go about their business without regard to the presence or absence of conspecifics and therefore do not constitute a social species; in fact, they are asocial. On the other hand, if the dispersion through space is generally non-random, then clearly the individuals are in fact responding to each other and we may safely conclude that the species represented by these individuals is social.

Non-random distribution can mean, at one extreme, that the animals are all clustered together into dense aggregates or, at the other extreme, that they are as widely dispersed from each other as possible so that they have in effect established something of a grid network. (Of course, combinations of the two extremes are also possible: clusters at various grid points, with maximal dispersion maintained between clusters.)

Clusters would constitute positively social groups in the homogenous environment that we have postulated, since individuals would not be likely to consistently cluster unless they were in fact responding to each other (the only non-homogenously distributed commodity in the environment). Individuals that are as widely dispersed (with respect to each other) as possible are negatively social (or unsocial), as distinguished from positively social were forces of attraction predominate.

When the environment is not homogenous (which it practically never is), then we are likely to find clusters of individuals wherein each is responding to some property of the environment rather than to each other (such as moths clustering around a light). In this situation, when the species involved is asocial, then the environmentally defined group is termed an aggregation. It is sometimes difficult to distinguish between an asocial aggregation and a positively social cluster. However, if the resources or environmental factors that draw the group together are dispersed (i.e., evenly distributed), then an aggregation of asocial individuals breaks up but a cluster of positively social individuals does not.

To recapitulate, then, in an absolutely homogenous environment, asocial animals are randomly distributed throughout the space while social animals are non-randomly distributed. Positively social animals are clustered in groups while negatively social animals are widely (but non-randomly) dispersed. In a non-homogenous environment, aggregations may be truly positively social groups or may be asocial individuals drawn together by some property of the environment other than each other.

Let me now offer some specific examples so that these terms may be more clearly understood. Suppose we released 50 houseflies (Musca

domestica) into a classroom. Chances are they would not be randomly distributed throughout the entire space available to them but instead would aggregate around the walls, windows and food sources (if any were available). Nevertheless, each fly would move about in complete disregard for the others except for an occasional mating; we could safely use the housefly as an example of an asocial species (putting aside, for the moment, the occasional matings that might occur).

If however, we had released 50 cows (Bos taurus) into an equivalent amount of space (say, a 500 acre field), they would more than likely maintain cohesiveness as a group and move about together. Should one be forceably separated from the group for a period of time, it would return to the group when the restraint is removed. The group as a whole would probably wander extensively, perhaps randomly, throughout the entire field but it would rarely if ever lose its cohesiveness as a group. These cows offer us a good example of a positively social species. Woodchucks (Marmota monax), on the other hand, are basically solitary animals outside of the breeding season. Had we released 50 woodchucks into the 500 acre field, they would have dispersed themselves around so as to maximize the distance between neighboring burrows; they are a good example of a negatively social species, at least during the nonbreeding portion of the year.

It is evident, therefore, that non-random distribution in space is an important characteristic of sociality, so long as a simple asocial aggregation can be distinguished from a positively social cluster. The basis for making the distinction lies in the responsiveness of individuals to each other. Let us now look at the "responsiveness" more closely.

Communication

Responsiveness means that an individual is not only cognizant of the presence of another, but is capable of adjusting its actions in terms of what the other is doing (and vice versa). Cognition is dependent upon perceptual capabilities (visual, chemical, auditory, tactile or various combinations thereof) and some internal means whereby the information can be integrated. At the simplest level, the adjustment called for may be mere approach or avoidance, but usually much more is involved depending upon the quantity and quality of information that is passed between the two. The system whereby each individual is capable of transmitting information to and receiving information from the other is termed communication, about which we will say much more later on. For the moment, though, let me state categorically that communication is the basis for social interaction; it is indeed the glue that holds social systems together. There can be no sociality without communication. However, the converse is not necessarily true: there can be communication without sociality. Communication signals that serve as attractants are sometimes mimicked by predators in search of prey.

Conspecifics

Having considered so far two important factors of sociality, spatial arrangement and communication, we turn now to still another property, that of population mix. Returning to our hypothetically homogenous 500 acre "Garden of Eden", suppose we had introduced a mixture of three different positively social species, say, a herd of impala (Aepyceros melampos), a flock of ostriches (Struthio camelus), and a troop of Anubis baboons (Papio anubis). It would not be long before the individuals sort

themselves out into three separate organized monospecific groups, with some but not much interaction between groups and much interaction within groups. Each species would occupy its own unique ecological niche so that the grounds for interspecific competition would be minimized even though the three species superficially show some general degree of niche overlap. Put in other terms, niche separation between species means far more extended and intensive intraspecific than interspecific competition. However, competition for available resources must be resolved, or at least attenuated, if the species is to survive. Sociality is a means whereby competition levels are contained (but not necessarily eliminated). It follows, then, that sociality should be primarily an intraspecific phenomenon and this indeed is the case. With one or two possible exceptions (to be explored later), sociality and social behaviors are restricted to interactions between members of the same species.

Adaptiveness

This brings us then to the crux of sociality: it is adaptive in that it contributes to the survival of the species by means of reducing levels of competition. Adaptiveness means that by and large individuals derive some sort of benefit from their interactions with others and the benefit permits them, on the whole, to be reproductively (i.e., genetically) more successful than they would have been otherwise. Mutual benefit implies co-operativeness, upon which is based modern concepts of sociality; Wilson (1975) defines a society as "a cooperating group of conspecific organisms", which is about the same definition used by earlier writers (Alverdes, 1927; Allee, 1931; Darling, 1938).

Sociality

We are now ready to weave together the four major characteristics of sociality discussed above to arrive at a reasonably good working definition of the concept with which we are dealing. Sociality is a system whereby the reproductive success of a group is enhanced by conferring survival advantage to at least some, if not all, members of the group. Increased survival advantages accrue through cooperative interactions among the members of the group, whereby each derives at least some benefit from the others. (At this point, it is not necessary to postulate that all derive the same amount of benefit.) Successful interactions among individuals depend upon effective communication systems that maximize the probability of a signal being appropriately interpreted. Effectiveness of the communication system and thereby of cooperative efforts and mutual benefits means that the individuals must be non-randomly distributed throughout the total available space.

II. THE SOCIAL BOND

Having described (if not defined) sociality in its broadest contexts, let us now examine in more detail the basic unit of sociality, the social bond. In grossest terms, social bonds exist if the behavior of an individual is consistently and continuously modified by the behavior of a conspecific; a social bond underlies the reciprocal interactions between two (or more) conspecifics.

More specific operational definitions of social bonds are usually based upon the context in which they appear and are simple descriptions of relationships that are commonly observed. The descriptive names of the pair associations characterize the type of association and are useful for discussions among ourselves, but they do not necessarily help us to understand the association. Nevertheless, labels such as parent-young bond and male-female (mated pair) bond have heuristic value even if the reverse, the young-to-parent bond and the female-to-male bond, may be significantly different.

Evolution of Sociality and Social Bonds

Aggregations are commonplace in nature: organisms "settle or collect in favorable localities, especially when the optimal niches are limited in extent" (Allee et al., 1949, page 393). The push or pull of nature is equally potent in the formation of aggregations of basically asocial animals: the push of wave action forms a drift aggregate along a shoreline, and the pull of an attractive fortuitous food source in the environment determines a feeding aggregate. In either case, it has been demonstrated that in some primitive forms, individuals in aggregates are

somewhat more successful in surviving and reproducing than nonaggregating individuals. There is no intuitive problem with this assertion: in sexually reproducing forms, gametes are more likely to encounter the opposite sex when the organisms issuing the gametes are in clusters rather than dispersed. But beyond the mere increment of probabilities of a sperm encountering an egg, Allee (1938) also found evidence for primitive, wholly non-conscious helpful interactions between organisms. He termed the phenomenon "proto-cooperation", and, among many examples, cites the fact that sea urchin sperm survive longer in dense clusters than they do when dispersed in sea water, and that many species of tropical aquarium fish do better in water in which other fish have been reared (so-called "conditioned water") as opposed to "clean" (or unconditioned) water.

It does not take too much imagination to go from simple physiological proto-cooperation to more extensive active cooperation and thence to full blown sociality. But while sociality itself is a very primitive phenomenon, almost as old as sex (without sociality there could hardly have evolved anything but the most happenstance forms of sexual reproduction), the forms of social expression, social systems and sociality itself have evolved independently in different groups of animals. Social structures have had to develop and operate within the limitations imposed by the niche occupied by the species. The highly social honeybees (Apis mellifera) are characterized by social structures that differ in many respects from other highly social animals (e.g., chickens).

Since sociality is based primarily on the idea of conferring a reproductive advantage, mating-pair bonds and parent-young bonds (even if only fleeting) must have been among the earliest social bonds to have evolved.

It would not take much to demonstrate the advantages of more enduring mating-pair and parent-young associations to produce not only more young but to enhance their chances of survival.

Measurement of Social Bonds

Despite the fact that we talk about a social bond as if it were something quite palpable, it is in truth quite intangible and eludes ordinary measuring techniques. Nevertheless, at least three indices have been used to gauge the intensity, if not reveal the mere presence or absence, of the social bond: one technique capitilizes on the fact that social animals are non-randomly distributed in space; a second employs behavioral and physiological measures of stress and disturbance; the third combines the aforementioned two into an operant paradigm.

Arrangement in Space: Inter-Animal Distance

If we were to crowd together a few cows (Bos taurus) or chickens (Gallus domesticus) so that they were in fact in direct bodily contact with each other, chances are that they would move apart when released from confinement . . . but they would not stray very far from each other. Similarly, if we were to release several cows (or chickens) at different points around a large enclosure, chances are that they would come together . . . but not too closely . . . before settling down to more routine activities. It is as if they were subjected to magnetic forces drawing them together if they are too far apart and pushing them apart if they are too close together. The resolution of the attraction and repulsion forces is some balance point (or more likely, a range of tolerance) wherein the individual neither moves towards nor away from its neighbor.

The distance from the individual to the balance point is termed the Inter-Animal Distance (IAD); it can be readily measured and, since it grossly reflects affinities between pairs of animals, it can serve as a useful index of the degree of sociality in the individual and in the group as a whole. Much as been written recently about "personal space" in humans; the same phenomenon seems to hold in nonhumans as well.

We must recognize, of course, that IAD can be influenced by factors other than social affinity and further that IAD is context related. Thus, a confined herd of cows in a paddock will necessarily stand closer to each other than they would in open pastures; similarly, during the colder months, they stand (or bed down) closer together than they do in warmer months of the year; if the range is sparse, they disperse more widely during grazing than if the range were lush; and so on. However, if factors such as temperature, time of day, season of the year, distribution of resources, etc., are controlled or at least taken into account, then IAD proves a useful tool in studying social bonds (and is the basis for Exercise 10, page 201). For example, IADs are age-related: young calves stay closer to their mothers than they do to other members of the herd, but the IAD increases with age to some stabilized point reached probably before maturity. Also, in sexually mature animals, IADs vary cyclically with the cycles of sexual receptiveity: at the peak of receptivity, the IAD approaches zero.

It should be recognized that IAD, in the way I am using it, centers on an individual: while we measure the distance between a pair of animals, the point of reference is only one of the pair. Since IAD is more likely a tolerance range rather than a fixed point, it is entirely possible that, observing two individuals sitting peacefully together (or

apart, of course), each may have a different acceptable IAD with respect to the other. When in fact the IAD (i.e., range of tolerance) of only one of them is violated, then there is movement towards or away from the other which in turn could reach the point where the IAD of the other is violated. We frequently observe this situation in Exercise 10, where the socialized quail continuously approaches the nonsocialized quail, which in turn moves away; the "chase" goes on for some time.

Exercise 10 (page 201)and its many possible variants provides the student with an opportunity to use IADs to measure the effects of social manipulations on subsequent social affinities. In our laboratory, we use Japanese quail (Coturnix coturnix japonica) because of its heartiness, small size and rapid development, but virtually any other conveniently available species may be used (provided sufficient space for testing is also available). The socially reared birds cluster immediately upon release and remain together throughout the period of observation (one or two hours); however, average IADs tend to vary directly with age up to maturity (six weeks in Japanese quail). Figure 1 shows the general relationship between IAD and age in socialized Japanese quail as observed in our laboratory.

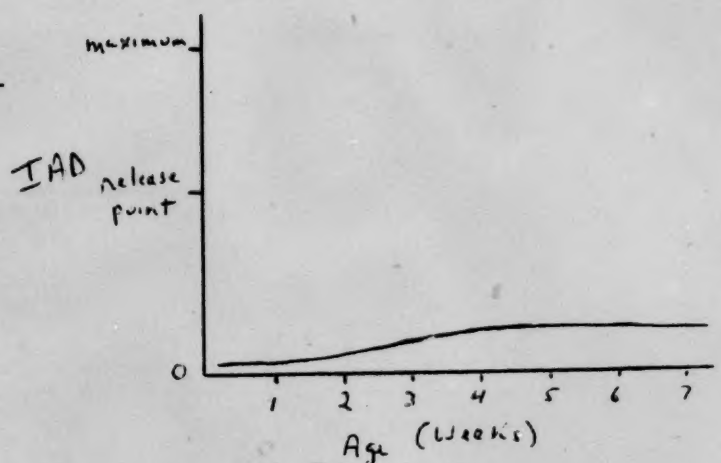


Fig. 1. The relationship between IAD and age in socialized Japanese quail.

Average IADs of socially deprived (visually isolated from the time of hatching) birds is related to the duration of isolation (or, put another way, that age at which the social deprivation terminates). Figure 2 depicts the general relationship between IAD and period of deprivation, as commonly observed in our laboratory during a one and one-half hour test session; the experimental animal is the Japanese quail.

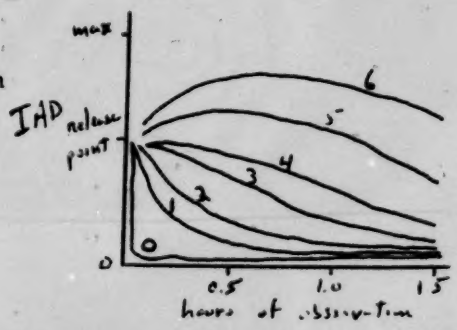


Fig. 2. IAD and period of social deprivation. Numbers indicate the number of weeks of isolation from the time of hatching; all birds are moved directly from isolation to the test arena so that the curves also represent different age groups; control birds are shown by the curve with zero weeks isolation.

It should be noted from the above set of curves (Figure 2) that socially deprived Japanese quail overcome the effects of deprivation relatively quickly, and that the younger the animal (or the shorter the period of deprivation), the more rapidly does the average IAD approach socialized control bird levels. Within an hour or two after the test begins, it is difficult for us to distinguish between socialized birds and those that have been deprived for one, two or even three weeks. It would be interesting to test other species in the same paradigm, especially those with significantly slower rates of development, to see if Japanese quail are unique in their apparent ability to overcome social deficits extending throughout at least half of their period of development to maturity. At the time of this writing, we have not yet tested the effects of social deprivation throughout the entire period of maturation.

In order for social deprivation to show the above (Figure 2) relation-

ship to IADs in quail, isolation must commence immediately upon hatching. I would anticipate that if acoustic as well as visual isolation could be imposed (especially if it started during incubation; see page 57), then the results would be even more clearcut and dramatic than those depicted above. Unfortunately, in our laboratory, only very limited acoustic isolation is possible. Social deprivation imposed after permitting several days (perhaps even hours) of post-hatching social experience has little or no demonstrable effect on IADs. However, it is possible that exceptionally prolonged periods of deprivation might in fact have an effect even after primary socialization is permitted. Again, different species could respond quite differently to postsocialization deprivations, and it would be interesting to determine at what point there might be a shift from reparable to irreparable effects of deprivation.

Emotionality

1. Physiological Measures. A second technique for measuring degrees of social affinities between pairs of animals, or at least detecting the presence or absence of a social bond, utilizes physiological manifestations or correlations /with emotional states. For example, it has been demonstrated a number of years ago that the output of adrenal corticoids from the adrenal cortex is directly related to the duration and degree of physiological insult imposed upon the animal. Thus, the more prolonged and greater the injury, the greater the adrenal cortical output. Like most endocrine glands, the size of the gland is also directly related to its output; hence, the more prolonged and greater the injury, the greater the adrenal size.

Others have found that physiological insult can be a direct result

of psychological or social stress. Putting all the correlations together, it follows that social stress should be directly correlated with, and therefore measurable by, the size of the adrenal cortex. And such is the case: Davis and Christian (1957, with mice), Siegel (1959, with chickens), and others found that the average adrenal size of animals in small groups is related to the group density, but the relationship is not purely linear (see Figure 3): within an optimal density range, the average adrenal (cortex) size varies only slightly with the density. At higher densities, however, average adrenal size steadily increases indicating increased social tension within the group. The curve eventually plateaus at some point beyond which further physiological adjustments to stress are not possible, i.e., individuals are forced to the limit of endurance and thereafter die.

It is interesting to note that a moderately social animal, like the laboratory rat, shows signs of stress when it is deprived of any social interaction (Group Size 1, Figure 3).

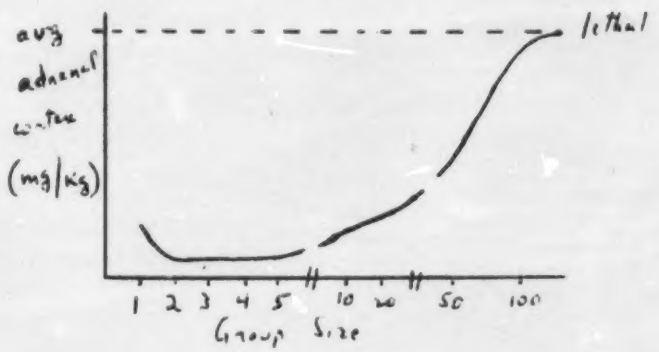


Fig. 3. The relationship between adrenal cortex weight and group size.

Adrenal cortex output (and therefore size) is also related to social status (see Hierarchies, page 86): individuals lower in the hierarchy are under more stress, and therefore have larger adrenals, than those in the higher ranks (Davis and Christian, 1957); these relationships are

shown in Figure 4.

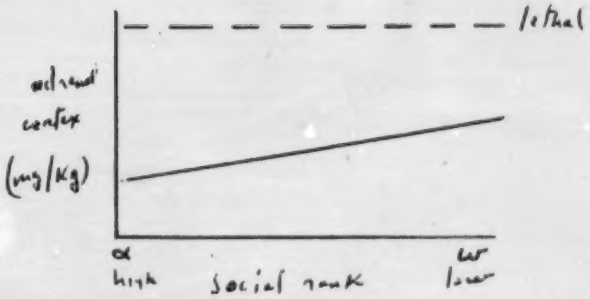


Fig. 4. The relationship between adrenal cortex weight and social rank.

Combining the observations depicted in Figures 3 and 4, it follows that at lower population densities, low ranking individuals have a greater chance of surviving than do their counterparts in high density groups; further, a high ranking individual in a high density group is probably under as much, if not worse, stress as is a low ranking individual in a low density group (Figure 5).

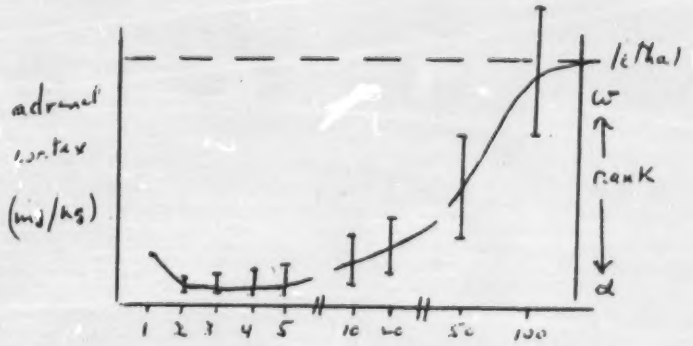


Fig. 5. The distribution of adrenal cortex weights in groups of different sizes.

It is interesting to note that in high density groups of rats, some individuals adjust to the situation by withdrawing completely from the social scene, i.e., they avoid and/or ignore interactions with other members of the group (Calhoun, 1971, /72). The survival rate of the social recluses is significantly higher than that of individuals that continue to compete in the social arena. Of further interest is the fact that social recluses retain their hermetic ways even when moved to more optimal density

situations (Calhoun, 1975), suggesting a long-lasting, if not permanent, effect of pathological levels of social tension.

2. Overt Physical Interactions. Another gross measure of social affinity is based on observations of intensities of physical interactions between individuals. In a series of studies, Guhl (summarized in Guhl, 1953) found that when a group of chickens is first assembled, the levels of interaction are initially very high: there is much fighting, threatening, chasing and general turmoil; both the rate and intensity of interactions are high. However, before long relationships between individuals become established and the intensity of interactions diminishes from bloody battles and fierce chases to simple threats and avoidances. Exercise 8 (see Section VII, page 192)is based on this phenomenon.

It should be noted that a marked decrease in the intensity of interactions (as measured along a spectrum ranging from a mild threat to a fierce bloody battle) does not necessarily signify a marked decrease in the total number of interactions: a group of cows in a highly competitive and socially disruptive situation might average about one pair-interaction per minute; the same group in a non-competitive, stable situation could still average about one pair-interaction per minute. However, in the former case the interactions observed are severe threats, fight, butts and chases, while in the latter case the interactions are mild threats and simple gestures.

Guhl was able to use the intensity of interactions as an index of social affinities and thereby measure such things as discrimination and retention abilities in chickens. For example, a strange outsider introduced to an established social group elicited immediate attacks and high

intensity interactions; the intensity of interactions remained high until the stranger became integrated with the group (i.e., was no longer a stranger). If, on the other hand, a member of the group was removed for a period of time and then returned, its reception back into the group was a function of the duration of its absence from the group. If the absence was short (a matter of hours or just a few days), it apparently was recognized by its colleagues as a member of the group and was not attacked; by the same token, it recognized its colleagues and the re-introduction was not marked by any undue concern. If, however, the period of absence was relatively long (a matter of weeks), then its return was for all intents and purposes the same as if a complete stranger had been introduced into the group. Apparently, retention capabilities of chickens for characteristics of their colleagues extends to only a few weeks, perhaps six weeks at most (Guhl, 1962).

The same technique was used to determine the characteristics whereby individuals recognize each other. Guhl (1962) found that recognition of individuals among chicks is based largely on visual configurations of the head and neck regions. An individual removed from a group and subjected to modifications of its body (blue paint, for example) was responded to as a normal routine group member upon its re-introduction to the group. However, modifications imposed on the head region (blue paint or an artificial, large rubber glove comb) resulted in its being treated as a complete stranger upon re-introduction. Recognize of course that the "complete stranger" syndrome was strictly one-sided: the experimentally modified bird still recognized its group mates and so entered the pen without hesitation; one wonders what went on in the unfortunate animal's mind when it was subjected to fierce attack by all its friends.

The situation was also reversed: one animal was removed from a group and then the head regions of all the remaining animals were modified. After a few hours (needed to re-establish relationships among themselves since they were suddenly strangers to each other) the unmodified bird was reintroduced. Its reaction was the same as if it had been introduced into a pen of strangers; it moved hesitantly, was exceptionally alert, and attacked those that approached too closely. The other members of the group however, obviously recognized their old colleague and seemed to be taken completely unawares by the severity of their friend's attacks. Again, one wonders what might have been going on in their collective minds as they encountered an obviously beserk comrade!

3. Vocalizations. In many species, sounds emitted by various individuals are context-specific; thus, a cat "purrs" when things seem to be going particularly well and not when it is being chased or otherwise engaged. In a vocalizing species, there are usually one or more characteristic sounds associated with duress. If the duress is occasioned by social factors, then a measure of the characteristic vocalizations can serve as an index of social stress. Such is the basis of Exercise 11(p.206), which uses "distress calls" of newly hatched precocial birds to determine minimal "acceptable" group size.

The usefulness of distress vocalizations as an index of social affinity was demonstrated by the work of Hoffman and his associates (e.g., Hoffman and Ratner, 1973). They found, among other things, that distress vocalizations of ducklings was suppressed by the presence of a mother or an appropriate mother surrogate. Removal of the mother (or appropriate surrogate) removed the suppression and the number of vocalizations

increased manyfold (Hoffman, 1968).

4. Droppings. By now it is obvious that any good measure of stress and disturbance can be used to gauge social duress. One more, counting droppings, has been particularly useful in working with laboratory rodents. Defecation is a not uncommon response to an uncomfortable disturbance, and Levine and his associates (e.g., Levine, 1962) used the numbers of fecal pellets dropped by mice to gauge degrees of stress: rats in unfamiliar environments deposited more pellets than those in familiar settings; similarly, mice confronted with strangers defecated more than those confronted with familiar penmates (Levine, 1962). There is little reason to suppose that this measure cannot be used with a greater variety of species and in more diverse local settings.

Preferences

A most direct measure of social affinities is to permit an individual to demonstrate its preferences in a free-choice situation. It can be used either as an all-or-none, presence-or-absence indicator or it can be used to quantify the degree of social affinity. Preference tests, properly staged, can be a powerful tool in the study of social behaviors.

In a number of studies, preference tests are the main instruments whereby the effects of social manipulations on subsequent behaviors are revealed. In our own studies (Schein and Hale, 1959; Schein, 1963), for example, newly hatched turkeys were imprinted either to turkeys or to humans. (The phenomenon of imprinting is discussed in greater detail below; see pages 41-60). They were reared together without regard to imprinting experiences, so that during the maturational period (and thereafter, in fact), each bird had ready access to its penmates and free and

easy interchange with humans (by virtue of almost daily visits for feeding, maintenance and observations). Upon reaching sexual maturity, the males were tested for sexual responsiveness following a short period (several days) of sexual deprivation. Confronted only with sexually receptive female turkeys, sexually active males responded with appropriate courtship movements and mating attempts, i.e., normal sexual behavior. Confronted only with humans in the test pen, the same males responded with the same courtship movements and mating attempts. However, when confronted with both sexually receptive female turkeys and humans simultaneously in the test pen, those males that had been imprinted to turkeys the year before devoted exclusive attention to the female turkeys while those that had been human-imprinted were equally devoted to the humans. Such sexual preferences were exhibited by both sexually naive and sexually experienced (with turkeys, of course) birds, and persisted throughout the lifetimes of the birds . . . in one case, 13 years (Schein, 1963).

Preference tests can also be used to reveal even more subtle manifestations of social affinities. In a series of studies now in progress in our laboratories, we are attempting to gauge the effects of various social experiences on the establishment and maintenance of social bonds. The basic premise is that the more the degree of social affiliation, the more time will the individuals spend near each other. For example, sexually mature (but not necessarily receptive) female African mouthbreeding fish (Tilapia mossambica) spend significantly more time near males of the same species than they do near males of even closely related species, regardless of their early social experiences or complete lack thereof (isolation reared) (Russock, 1975).

With small birds, such as Japanese quail (Coturnix coturnix japonica), we use a test box of the general design depicted in Figure 6.

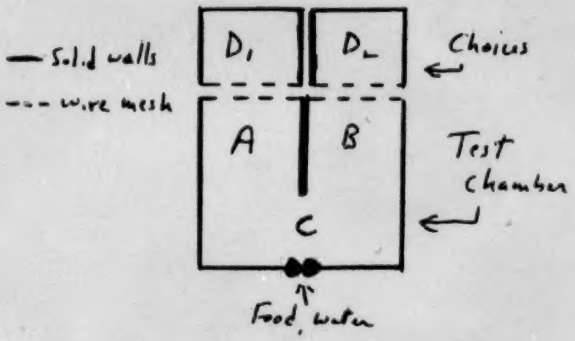


Fig. 6. General design of a preference testing cage.

In a current series of experiments dealing with sexually mature adults, the test bird lives in the test chamber for a 4-day period; it has completely free access to sections A, B, or C of the test chamber. An open-mesh wire separates the test animal from the discrimination cages D_1 and D_2; a Japanese quail of the opposite sex is placed in one discrimination cage and a Bobwhite quail (Colinus virginianus) in the other. Bobwhite quail are almost double the size of Japanese quail, have roughly the same general configuration and body color, and have moderately different markings in the head region. The right-left positions of cages D_1 and D_2 are alternated daily so as to be able to distinguish between a position preference as opposed to a partner preference on the part of the test animal. Some birds exhibit a strong position preference (or a reluctance to move about) during the first day or two of the test, but most adapt to the situation relatively rapidly and move freely about the test box. All birds are subjected to at least two and in some cases as many as four "runs" in the test box.

Results so far indicate a great deal of individual variation, perhaps more than was initially anticipated. Early social experiences (rearing

either by foster Japanese or foster Bobwhite quail mothers, or simple rearing with siblings in a brooder without adults present) had no discernable effect on social preferences as adults. Many of the birds showed no real "stay-near" preferences; they spent roughly equal amounts of time with each of the possible partner choices. However, males on the average spent more time with a partner (either in the A or B section of the test box; see Figure 6) than did females, who spent somewhat more time (at least initially) in the C postion of the test box (perhaps avoiding either choice). It is probably significant to note that the birds were not sexually deprived as they entered the test box; by the end of the test, on the fourth day, the males showed strong evidence of sexual deprivation but the females much less so.

Of those birds that did show strong preferences for one species over another, males generally preferred Japanese quail partners while females exhibited broader tastes. It might be suggested that size differences between the two species could affect the choice, but we have observed sexually deprived Japanese quail males mount and attempt to mate with much larger struggling Bobwhite quail on a number of occasions.

In a closely related study using the same basic test design (see Figure 6), young Japanese quail were confronted (over an 8-hour period) with a choice between a cage containing a bird of equal age (D_1) or an empty cage (D_2). As expected, those birds reared together in social groups, the controls, clearly exhibited strong preferences for the side from which they could see (and stay near) their peers. However, the total quantity of "stay-near" time diminished somewhat with age up to maturity (at 6 weeks). Those birds that were reared as visual and social isolates (similar to the conditions described in Exercise 10, to which this study

is related) either avoided or ignored age-mates at the outset, but strong affinities usually developed before the 8-hour test period was concluded; the younger were the birds at testing, the sooner during the test period were the affinities revealed. Thus, one week old socially deprived birds overcame their social deficiencies within an hour or two, while three and four week old deprived birds needed four or five hours to develop an attachment for the stranger (Table 1).

Other questions that we are seeking answers to relate to the formation, maintenance and dissolution of bonds between parents and young (and vice-versa), between mating pairs, and between familiar versus unfamiliar conspecifics. While the initial studies were designed to answer questions relating to the effects of early social experiences, preliminary results indicate that we have gotten answers, at least preliminary answers, to questions that we have not yet asked. Indeed, our problem might now be to discover the questions that relate to the answers we have at hand.

Establishment and Maintenance of Social Bonds

There are three primary phases that must be considered in the study of social bonds: the formation, the maintenance, and the eventual disruption of the bond. Each of the phases involves factors and behaviors unique to that phase, which when combined offer perhaps an insight into the mechanisms and principles underlying social interactions. Let us examine first the establishment of social bonds.

The Associative Learning Model: Familiarization

An individual that suddenly confronts another for the first time is immediately thrust into a threatened position: the stranger may approach, avoid or simply ignore. If the stranger approaches, then defensive behavior of one sort or another may be called for; if the stranger ignores or avoids, then different constellations of responses are put into motion. If the stranger is not a member of the same species, then responses are more or less merely limited to approaches, ignorings, or avoidances. However, if the stranger is a conspecific, then refinements of the triad (approach, ignore, avoid) are possible by means of reciprocal communication. With appropriate signalling, it can be determined whether or not an approach is something to be feared or not, and an ignore and even an avoidance might be converted into an approach. In this manner, the initial potential threat is removed and the stranger is no longer a stranger but a familiar, to be used or ignored as the context demands; a loose bond can be said to exist.

If the situation arises where each derives some special benefit from the other, above and beyond their simply being members of the same group, then the bond may strengthen. A seasonal mating pair-bond serves as a good

example of a situation whereby each partner derives benefits from the other in terms of the production and enhanced possibilities of survival of progeny. When the young have matured enough to go forth on their own, the mating pair-bond often dissolves, although in some species that "mate for life", the pair-bond does not completely dissolve and is reinstated each breeding season (e.g., albatrosses, as described by Fisher, 1968).

The basis of such social bonds is simple associative learning: once the possibilities of mortal danger are eliminated or at least significantly reduced (the familiarization process), then it is possible to associate certain benefits with certain individuals, provided it is within the realm of capabilities to distinguish one individual (or at least one class of individuals) from another. The more benefits derived by each partner, the stronger and more exclusive is likely to be the social tie. Associative social bonds can be formed between any pair of individuals or even among groups of individuals, provided generally equal benefits accrue to each.

Since associative social bonds are based on simple learning, some sort of reinforcement schedule is necessary to prevent the extinction of the learned association. The schedule of reinforcement depends upon the retention capabilities of each partner: those with very short retention capabilities will need more or less continuous reinforcement, while those with good memories will only occasionally have to be reminded of the configuration of their "friends". In an interesting film depicting the habits of butterfly fish on coral reefs (Reese, 1974), the author noted (Reese, personal communication) that those fish that operated together in pairs (whether mated pairs or not is unknown) continuously "checked" with each other by visual (and sometimes bodily) contact, and especially after momentary separation by some feature of the terrain. Fisher (1968)

ascribes the elaborate courtship ceremonies of a mated pair of albatrosses at the beginning of each breeding season, as well as the nest-relief ceremonies during the course of the season, to a reinforcement or refreshing of a bond that was established long before. Similar examples of continuous "cross-checking" in many other species would not be hard to come by.

Although, as mentioned above, associative social bonds are primarily intraspecific phenomena because of the crucial role that communication plays in establishing and maintaining the bond, it is possible to conceive of situations where a sufficient level of interspecific communication can be achieved thereby permitting the establishment and maintenance of an interspecific social bond. Such is likely the case with people and their pets: the relationship is mutually beneficial and sustained by at least minimal levels of reciprocal communication. The human-pet relationship is probably one of the few exceptions to the general statement (see page 20, above) that sociality is primarily an intraspecific phenomenon.

The Imprinting Model

Naturalists have long noted that the young of many species show profound behavioral effects of cross-fostering experiences: the patterns of behavior exhibited by the cross-fostered animals are well organized and perfectly appropriate to their own species, but the behaviors are elicited often by biologically inappropriate stimuli. For example, courtship and other social behaviors of an individual that had been cross-fostered by a member of another species would more likely (and perhaps even exclusively) be directed to members of the other species rather than its own. This

general phenomenon was termed "Prägung" by Lorenz (1935), which was translated into English as "Imprinting" (Lorenz, 1937); it refers to the process whereby certain information from the environment is "stamped into" the newly hatched young and thereby forms the basis for social attachment of social behaviors. The first object to elicit a social response from the young bird, later released social and related (sexual) behaviors. (Lorenz dealt originally with precocial birds, ducks and geese, and much of the research that followed his classical landmark paper concentrated on precocial species).

Reviews of the history of the imprinting concept and its present day status are provided among others by Bateson (1966, 1971) and Hess (1973, 1976). In the original formulation of the imprinting phenomenon, four major characteristics were postulated that, when taken together, made imprinting an unique phenomenon:

(a) Imprinting can occur only during a very brief and definite period in the life of the individual; the period of sensitivity to imprinting is so sharply defined as to constitute a "critical" period.

(b) The effects of an imprinting exposure are irreversible and persist throughout the lifetime of the animal.

(c) The imprinting process itself is completed long before specific reactions stemming from its effects are called for.

(d) What is imprinted is not necessarily the detailed characteristics of an individual or an object but instead a general class of individuals or objects to which the imprinted animal will subsequently direct social responses; imprinting is supra-individual learning.

Controversy still rages over each of the four characteristics, chiefly the first two (critical period and irreversability) and a number of workers have concluded that imprinting is nothing more than a peculiar form of learning restricted to precocial species. On the other hand, others (e.g. Hess, 1973, 1976) maintain that imprinting is indeed an unique phenomenon, that it links innate predispositions for specific environmental influences with genetically endowed learning capabilities, and that it has far more widespread application throughout the animal kingdom (including primates) than merely a handful of precocial species (e.g., Hoffman and Ratner, 1973).

Each of these characteristics has been studied by itself and in combination with others, and each has been disputed and refuted or supported and confirmed depending upon which investigators one follows; the issues are far from settled even today. It is not my purpose here to re-review the literature on imprinting nor to enter into the controversy as to what imprinting is or is not, but rather to examine the observed phenomenon in terms of sociality and social bonding.

In a typical imprinting experiment, if any experiment can be considered typical, a newly hatched Mallard or domestic duckling (several hours post-hatching) is exposed to a moving object in a large circular runway; control ducklings are placed in the runway but the moving object is absent. Up until the time of exposure, neither the experimental nor the control birds had ever experienced mobile objects in their environment. Removal to the circular runway is in itself traumatic, and birds normally reflect the trauma by issuing distress calls. Such calls are present in the control birds until they adjust to their new environment, but terminate rather rapidly in the experimental birds as their attention

becomes focused on the moving object. Almost immediately upon becoming aware of the moving object, experimental birds approach it and more or less attach themselves to the object. Distress calls cease when they are near or hovering under the object, and are emitted again if the object passes from immediate view or moves too far away.

Following the relatively brief exposure period, perhaps as short as 10 minutes, the birds are returned to their solitary home cages. Four or five days later, the birds are tested to see if the early exposure had any effect: experimental and control birds are placed in the circular runway again, but this time the moving object is present for both types of birds. Control birds, who are confronted with the object for the first time, flee from it and emit distress calls, but experimental birds approach and follow the object as it moves around the ring; if they vocalize at all, it is with soft chuttering sounds (known as "contentment" calls) rather than with distress calls. Thus, a very brief exposure during the first day post-hatching has a clear and demonstrable effect five days later.

Much of the earlier imprinting research used the basic design outlined above and dealt therefore with young precocial birds on a short-term basis. The proximity that the young bird maintained with the imprinting object, by means of following it about, constituted a measure of the strength and degree of imprinting. Other measures, such as latency to approach and extent and type of vocalizations were also employed, but "following", which is basically a measure of IAD (see pages 24-28), was the primary gauge.

Using such techniques, it was determined that under normal (laboratory) circumstances, young ducklings may be imprinted up to approximately

32 hours posthatching, but the peak of sensitivity (a critical period) occurs at 13-16 hours after hatching (summarized in Hess, 1959, 1963) or so hours after the onset of incubation (Gottlieb, 1963), which coincides roughly with 13-16 hours after hatching. The period of sensitivity can be extended an additional day or two by maintaining the newly hatched birds under visual as well as social deprivation conditions for their first 24-48 hours posthatching; newly hatched chickens, ducks and geese have enough reserves in the yolk to sustain them without additional food or water for approximately 3 days posthatching.

Hess (1959), and then later Hoffman and Ratner (1973), postulated that the decline of sensitivity and the extent of the sensitive period was determined primarily by the maturation of a fear and avoidance response to novel stimuli; avoidance is notable by 24 hours posthatching and fully developed by 48 hours (Figure 7). At the other end of the spectrum, birds much younger than 10 hours posthatching are not sufficiently well coordinated as yet to engage in sustained efforts to achieve continuous proximity to moving objects.

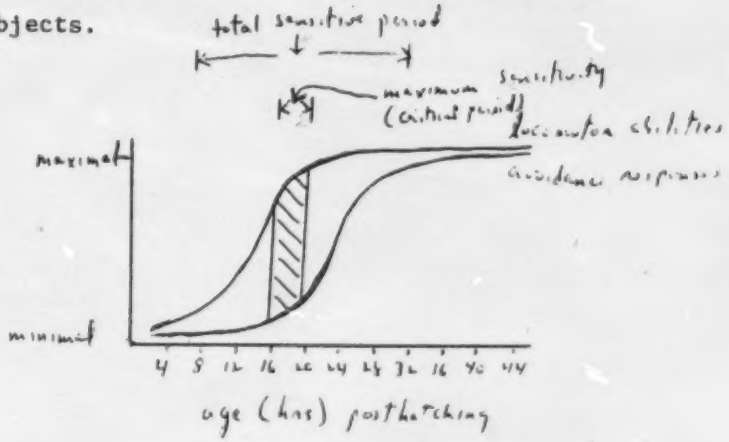


Fig. 7. Maturation of locomotor abilities and avoidance responses in chicks and ducklings.

In terms of the natural situation, it makes good sense for a short time gap to exist between the development of locomotor abilities and the maturation of fear and avoidance responses. The precocial animal needs

to very quickly develop a fear and avoidance response to strange and new objects, especially objects that move, but the maturation of the avoidance response cannot occur so rapidly as to preclude the development of some sort of filial attachment.

The behavior of the imprinted individual is profoundly modified by its early experience; hence, imprinting has been equated to learning. However, Hess (summarized in Hess, 1973, 1976) pointed out several significant differences between "imprinting learning" and ordinary associative learning. Among the differences listed by Hess:

(1) Associative learning is best effected under spaced rather than massed exposure routines. That is, the animal learns best if the total quantity of exposure time is broken up into a number of short learning periods; in imprinting, just the reverse is ture: the animal imprints best if it receives all its exposure in one session rather than in a series of short exposures.

(2) In associative learning, recency is more important than primacy. Retention is stronger for those things learned more recently; the last thing learned is best remembered. In imprinting, the converse is true: primacy is more important than recency. Retention is strongest for the thing to which the animal was exposed first.

(3) In associative learning, punishment generally has a negative effect: punishment is a good way to get the animal to <u>avoid</u> something. In imprinting, Hess (1959) found that 'punishment' generally had a positive effect: the harder the animal had to work to achieve proximity to the imprinting object, the stronger was the resultant imprinting attachment. Hess' Law of Effort,

Is = log E (where Is = strength of imprinting and E = effort expended), is based on these findings.

Failure to recognize the distinction between the types of bonds formed as a result of associative learning and those formed by 'imprinting lea ing' and failure to recognize the roles played by each in the total formation of a social bond, coupled with a distinct disregard for the natural history of the species under study, has led to much apparent contradiction and controversy in the study of imprinting. For example, if 'following' is used as a measure of imprinting, then the effects of imprinting appear to dissipate well before the individual reaches maturity; few animals strive to maintain virtually zero distance between themselves and a parent (or surrogate) throughout the entire course of their development. (As we have noted earlier - see Figure 1, page 26 - the tolerable IAD steadily increases with age.) In fact, it is not necessarily the imprinting effects that have been dissipated but rather the phenomenon of 'following', which for older animals no longer serves as a measure of imprinting. (Indeed, in a number of species and especially altricial animals, 'following' is a useless measure since the young typically do not follow parents about.) A stronger and in the long run more useful measure of imprinting, that has found more widespread application in later research, has been the denotation of partners in various social endeavors. Sexual behavior is most commonly used in this respect, since the behavior patterns are generally clearly defined and the expression of partner choice is generally definitive.

Another source of confusion and apparent contradiction in the literature has been the extent of control that imprinting was assumed to exert over social interactions. However, much of the contradiction disappears

when it is recognized that imprinting affects the preferential rather than the exclusive responses in social behaviors. An illustration of the point has been presented earlier in the discussion of the use of preferences to measure social affinities (see pages 34-38).

If social bonds can be formed on the basis of ordinary associative learning, with all its implications with respect to rules of acquisition, retention and reinforcement schedules, what then is the role of imprinting in social behaviors? We proposed a model some years ago (Schein, 1963) that we believe can still account for many of the observations in imprinting research and provides a resolution for a number of apparent contradictions. The model draws upon the original Lorenzian formulations and extends them to incorporate the important function of ordinary associative learning. The basis of the model is the proposition that general species-typical characteristics are 'learned' during the imprinting exposure by some unique imprinting learning process - perhaps akin to Seligman's (1970) 'prepared' learning; acquisition rates are exceptionally rapid compared to those observed in associative learning. Further, what is learned during the imprinting exposure is exceptionally stable: extinction rates are negligible, certainly in comparison to extinction rates observed in associative learning paradigms. However, the characteristics of specific individuals, such as parents or various group members, are learned by means of ordinary associative processes with standard rates of acquisition and extinction and therefore the necessary periodic reinforcements to bolster retention.

Under natural conditions the difference in rates of acquisition between imprinting and associative learning is not detrimental to the young, and in fact may be beneficial in certain situations. The youngster

very quickly learns the general characteristics of the species to which it belongs (imprinting learning) and at a much more leisurely pace learns the characteristics that distinguish its own parent from other parent figures; it is on this latter basis that the very specific young-to-parent (and probably parent-to-young) bond is formed. Should some disaster befall the parent before the young-to-parent bond is formed, it is of no major import to the youngster which will readily adopt any other available parent, but a parent of the appropriate (imprinted) species.

Our own observations of chickens and turkeys suggest that the chicks do not recognize their own parents for perhaps as much as a week or two after hatching; they will approach and stay near any non-threatening adult bird in the vicinity, and will respond positively to the 'come hither' calls of any parent, even to the point of ignoring their own mother who may be competing with another parent for the young. At the same time, it is my impression that it takes the chicken or turkey parent some time, perhaps a week or so, to be able to distinguish its own young from others. Parents readily adopt (and are adopted by) offspring from other parents during the first week or two after the young have hatched. These and related phenomena are readily demonstrable in Exercise 3 (see page 175).

It should be recognized, of course, that in some species, particularly those that produce few offspring, the rate of acquisition by the parent of the characteristics of its young, and probably vice versa, are significantly faster than in chickens and turkeys. For example, goat, sheep, deer and cow mothers appear to be able to distinguish their own young from others (on the basis of olfactory cues) within hours after birth.

Collias (1956) reported that newborn lambs or kids removed from their sheep or goat mothers for as little as three hours following birth were rejected by their mothers. If, on the other hand they were removed for only an hour or less after birth, they were all accepted by their mothers. These parents nurse only their own offspring, although the young will attempt to feed from any parent (at least for a time, until negative reinforcement in the form of chastisement teaches them that only one food source is available to them).

In a laboratory setting, it is relatively easy to manipulate the imprinting and associative learning possibilities and thereby be able to study the effects of each either independently or in combination. The scheme offered in Table 2 is based on the model proposed by Schein (1963) which showed 12 basic combinations of imprinting and associative learning. An individual of a given species, S, is imprinted either (1) to its own species; (2) to some other species, O, to which S will readily imprint under the proper conditions; or (3) to nothing, i.e., it is socially deprived during the sensitive period for imprinting. Following the termination of the imprinting-sensitive period, the animal is reared either (1) exclusively with members of its own species; (2) exclusively with members of the other species, O; (3) with members of both species S and O; or (4) under conditions of complete social deprivation. The rearing period is sufficiently long to permit 'familiarization' (the formation of associative learning bonds) to occur. Predictions of social interactions and preferences (as indicated by sexual behaviors) for various combinations of imprinting and familizarization experiences are shown in Table 2.

Table 2. The imprinting-associative learning model: predicted social (sexual) preferences

	TREATMENT		TESTS			
			(1) Sexual responses when confronted only with		(2) Preference when confronted with both	(3) Preference after familiarization with both
CONDITION	Imprinted to	Familiarized with	S	O	S + O	S + O
1	S	S	+	-	S	S » O
2	S	O	-	+	O	S > O
3	S	SO	+	+	S > O	S > O
4	S	X	-	-	-	S » O
5	O	S	+	-	S	O > S
6	O	O	-	+	O	O » S
7	O	SO	+	+	O > S	O > S
8	O	X	-	-	-	O » S
9	X	S	+	-	S	S > O
10	X	O	-	+	O	O > S
11	X	SO	+	+	S = O	S = O
12	X	X	-	-	-	S = O

NOTES: S: own species
O: other species
X: social deprivation

+: sexual response
-: no response or avoidance

>: greater than
»: much greater than
=: no preference; each equally acceptable

Condition 1 (Table 2) where the animal is imprinted to and familiarized with its own species exclusively, represents the normal natural condition. Such animals direct social interactions exclusively to members of their own species and avoid or are indifferent to members of other species. If familiarization with another species is subsequently imposed, then some secondary social responses to the other species may be observed.

Condition 2 might be likened to some of our pet dogs, dogs that are separated from their mothers at weaning and thereafter reared in a city apartment where they have no opportunity to encounter other dogs. Their social interactions and sexual advances are directed exclusively to humans, the only social beings with which they are 'familiar'. If confronted with a real dog later in life, they are very likely to react with terror at first, but can subsequently be 'tamed' to dogs.

Condition 3 is well represented by the control turkeys described earlier (see pages 34-36). These birds had been imprinted to turkeys but reared with turkeys and humans. They directed sexual and social responses to either species in the absence of the other, but preferred turkeys when offered a choice. Just the reverse choice was shown by the experimental (human imprinted) turkeys, as represented by Condition 7.

The initial individual and preference tests would not permit a distinction to be made between animals subjected to Conditions 1 and 5, 2 and 6, or 4 and 8; the difference would only become apparent in a preference test that followed a period of dual familiarization.

Conditions 9, 10, 11 and 12 are interesting in that the animals are not imprinted: each is maintained in social isolation until the sensitive period for imprinting is well over. Recovery from such social

deprivation is possible, as we have seen earlier (see Figure 2 and discussion on page 27). Thus, prior to subsequent dual familiarization, animals subjected to Condition 9 or 10 are indistinguishable from those subjected to conditions 1 and 5, or 2 and 6, respectively. Following dual familiarization, animals from Condition 9 (or 10) should exhibit different preferences from those of Condition 5 (or 6) and perhaps be distinct from Condition 1 (or 2) animals in terms of the intensity of responses.

The model predicts that it should be relatively easy to identify Condition 11 animals as distinct from those subjected to Conditions 3 and 7 on the basis of their not exhibiting any real preferences: the species with which they interact in a preference test seems to be determined more by chance than by choice. The few animals that we have been able to rear in Condition 11 (unimprinted chickens reared with both chickens and turkeys) seemed to show just such traits (Schein and Hale, 1965).

Condition 12 represents the extreme: an animal completely deprived of any social interaction throughout its period of growth and maturation. Those chickens and turkeys that we have been able to rear to maturity in such conditions (for various reasons, survival rates are not high) are indeed different: they exhibit proper <u>patterns</u> of sexual and social behaviors, with all the appropriate sounds and postures, but the patterns are not released by readily identifiable components of the environment. In other words, we do not recognize the stimuli that trigger their social behavior patterns. We have observed (surreptitiously, of course, since these animals exhibit extreme anti-predator responses to other animals, including members of their own species) Condition 12 turkeys 'courting'

inanimate objects (e.g., lightbulbs, food cups) or just plain courting in an absolutely barren environment. Thus, while their responses during the initial individual and preference tests are similar to those exhibited by animals subjected to Conditions 4 and 8 (except perhaps that their avoidances might be far more pronounced), following a period of dual familiarization they should exhibit the equipotentiality of Condition 11 animals.

It might be appropriate to ask how widely the imprinting model can be applied; is the phenomenon limited to precocial forms, such as a few bird and mammal species, or does it extend to altricial forms as well? Does it extend further along the phylogenetic spectrum than simply birds and mammals? In answer to the first question, there is evidence of imprinting in several altricial species, including Rhesus monkeys, guinea pigs, finches, and doves, among others. The difficulty in working with altricial forms is that the individual is well imprinted long before weaning or fledging, so that to demonstrate the phenomenon it is necessary to cross-foster or hand-rear the youngster. Hand-rearing is at best a tedious proposition, and especially with animals other than a young primate, so cross-fostering is the technique more commonly used. In an ingenious series of such experiments, Immelmann (1973) determined that the critical period for imprinting Bengalese (Lonchura striata) and Zebra (Taeniopygia guttata) finches was 18 (± 1/2) days after hatching. This time coincides exactly with the age at which the young birds, which are hatched naked, blind and utterly helpless, finally open their eyes. Apparently, they direct all social behaviors to whichever species confronts them when they first open their eyes, no matter which species has been tending them up to that point.

The answer to the second question, that of the applicability of the

imprinting model along the phylogenetic spectrum, is perhaps more difficult to come by and will require patient gathering of data from a number of species. For example, the recent studies of homing in salmon suggest that some form of imprinting occurs in at least some species of fish. On the other hand, a study of the African mouthbreeding fish (Tilapia mossambica) failed to reveal any demonstrable effects of imprinting-type exposures, or deficits as a result of lack of exposure: fish hatched and reared to maturity in complete visual isolation still preferred their own species in visual preference tests (Russock, 1975). Thus, innately determined responses cannot be ruled out, even if we do not as yet know or understand the mechanisms involved.

Do humans imprint also? The question may necessarily have to remain unanswered because of the impracticality of designing imprinting-type experiments with humans as experimental subjects. Nevertheless, on the basis of experiences with other primates, a number of researchers (e.g., Bowlby, Slukin and others) are confident that humans imprint to humans in the same manner as do other species.

What in fact might be the mechanism underlying imprinting learning? And how is it that some species are easily imprintable in the laboratory while others are not? Griswold (1971) has proposed a functional validation model based on ideas put forth earlier by Jacobson (1969), wherein the young of each species are born (or hatched) with some sort of innate "schemata" built into their systems. It might be that their perceptual capabilities at birth are particularly attuned to certain inputs, and under normal conditions the innate "schemata" will be "validated" by environmental conditions. Validation may come in the form of visual, auditory, chemical or tactile signals (or some combination thereof),

and if validated, the innate schemata will become fixed in the animal's central nervous system and the animal is thereby imprinted. However, unless validated the innate schemata dissipates fairly rapidly and the animal is no longer imprintable (but is still amenable to social bonding by means of ordinary associative learning).

There is some evidence for the idea of an "innate schemata": in some species, imprinting can be effected with objects ranging widely in visual, acoustic and chemical characteristics; other species are not so tolerant and the imprinting object must fairly closely approximate the natural parent; in still other species, imprinting can only be achieved with the proper parent species. In the first case, typified perhaps by surface-nesting ducks and geese, the "innate schemata" would be quite broad, with only a few parameters (such as movement and general size, perhaps some sounds) being of primary importance; in the third case, perhaps typified by the unimprintable curlew (Numenius spp.) the innate schemata would be very sharply defined, matched only by an adult of that species. Differences in the definitiveness of the "innate schemata" could have important adaptive significance: newly hatched ducklings and chicks are not likely to be confronted with other species models during the imprinting period and therefore can afford a very lax schemata; other species that typically nest in mixed species environments (various marine birds, for example) may very well need sharply defined schemata in order to ensure appropriate subsequent social behaviors.

It is clear that the imprinting model cannot be universally applied. Parasitic birds, such as European cuckoos (fam. Cuculidae) and cowbirds (Molothrus ater) lay their eggs in nests of other species; therefore, the young do not encounter members (or at least

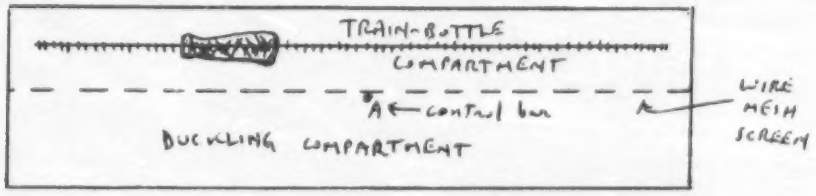
adults) of their own species until after fledging. Still, they successfully mate and socialize with each other despite being cross-fostered by another species. There is some suggestion, however, that the adults of parasitic bird species tend to parasitize those species with which they have had experience as young; whether or not this observation reflects some form of imprinting remains to be established.

The Mallee fowl of Australia (Leipoa ocellata) offers a clear example of a case where imprinting certainly cannot occur. These birds are incubated in sand mounds and have essentially no contact with their parents. Upon hatching, they emerge independently from the mound and scamper off into the bush where presumably they go about the business of surviving without the necessity of socially interacting with adults or perhaps even with siblings. In this sense, their social responses must be as innately determined as the African mouthbreeding fish described earlier (see page 55).

That the "innate schemata" may not be so completely innate could be inferred from the works of Kuo (1967), Hess (1973), Gottlieb (1971) and others. Prehatching experiences have a decided effect on subsequent posthatching behaviors. For example, although mallard ducklings do not hatch until about the 27th or 28th day of incubation, they are able to emit vocal signals a full day or two before hatching. The incubating parent attends to these signals and vocalizes in return. That the pre-hatched duckling is able to hear the parents' signals is demonstrated by the fact that newly hatched ducklings respond to, and imprint much more quickly and strongly to, signals that they were exposed to a day or two pre-hatching rather than to signals that they are exposed to for the first time only after hatching (Hess, 1976).

Finally, the work of Hoffman and his colleagues (e.g., Hoffman, 1968) serves as an example of the uses that can be made of the imprinting phenomenon in the study of social behavior. Newly hatched ducklings were imprinted to white plastic milk bottles mounted horizontally on a toy electric train that reversed its motion whenever it reached the end of the compartment. In the basic exposure setup (shown in Figure 8), the duckling is separated from the moving mild bottle by a mesh screen, and lighting is so arranged that it can see the milk bottle only when the bottle compartment is illuminated; the lights and train movement are so linked that the train moves only when the lights are on in the bottle

Fig. 8. Imprinting set-up used by Hoffman and colleagues.



compartment. The distingushing feature of Hoffman's original setup was the inclusion in the duckling compartment of a bar (marked A in Figure 8), which, when pecked, turned on the light in the bottle compartment and activated the train for some short period of time. Thus, after a very brief period of "shaping" the duckling to peck at the bar (by the technique of successive approximations), the duckling had complete control of the exposure situation. Most ducklings learned the keypeck response after only a very brief exposure to the moving stimulus; they in fact very rapidly shaped themselves to peck the bar. Once the ducklings controlled the situation, studies of the development and maturation of

filial (care-soliciting) behavior could proceed apace. For example, a duckling might follow a period of quiet resting with a few mild distress calls and then a bar press that activated the lights and train. Distress calling would terminate as soon as the stimulus was activated, but might start again as soon as the stimulus presentation was terminated; the calling might persist until another bar peck brought forth the stimulus again.

The extent to which the stimulus was called forth, as measured by the rate of bar pecks per day or hour, tapered off markedly as the ducklings matured. (The general relationship between bar pecking and age is shown in Figure 9). It was surprising to note, however, that bar

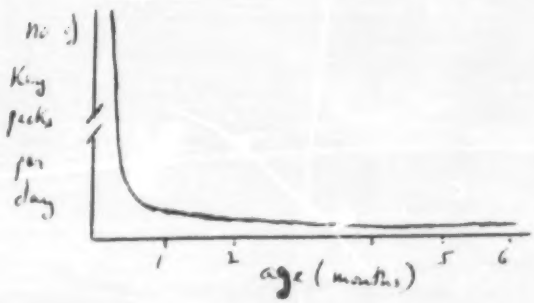


Fig. 9. The relationship of keypecks to age in imprinted ducklings.

pecking did not extinguish completely and persisted well beyond the first few months of age (Hoffman and Koszma, 1967). At any point, the imposition of behavioral stress resulted in an immediate burst of bar peckings. For example, if a bird was suddenly confined to one end of the compartment, it became increasingly agitated and continuously emitted distress calls; upon release, it would run directly to the bar and peck repeatedly until it appeared to "calm down". The same effect could be accomplished by denying the bird access to a favorite resting site or box in the test compartment; it would immediately go to the bar, bring forth a few presentations of the milk bottle stimulus, return to the

denied box for another try, and if fruitless, return to the bar for more pecking. It is difficult to resist anthropomorphic interpretations of these observed behaviors.

Types of Social Bonds

It might be assumed from the preceeding discussion that any member of a population may form an association, a social bond, with any other member, and so it is. Still, bondings are not as randomly distributed as they potentially could be: certain associations are more typically observed than others. Put another way, some types of associations are common to virtually all social structures, and others are specific to particular kinds of social structures. Let us look first at relationships between and among individuals, then at relationships involving groups, and finally at some interspecific social relationships.

Bonds Between Individuals

1. Parent-Young Bonds. Parental behavior is indigenous to all social systems, but the types of bonds established and the participants in the bonding vary among species and social structures. In mammals, where nursing by the female parent is obligatory to survival of the young, a mother-to-young bond is typical. In many mammalian species, the mother-young bond constitutes the major expression of parental behavior: fathers rarely form bonds with infants. In some mammalian species, however, where the social structure centers around family groupings (e.g., wolves, foxes), fathers do play a role in the care of the young and so some sort of father-young bond must be formed. It

should not be overlooked that adoption, even kidnapping, may not be so rare, especially among the primates. There are many reported instances of maternal behavior being exhibited by adult female rhesus monkeys who adopted an orphan or actually stole the baby from its real mother.

Maternal bonds may be very tight and exclusive or may be loose and permissive. Bonnet monkey (Macaca radiata) and Black-faced vervet (Cercopithecus aethiops) mothers are very relaxed: other adult and even juvenile females are permitted free access to their infants for purposes of handling, grooming and even carrying about. Thus, brief periods of mother-infant separation are not especially traumatic events to either the mother or the infant, who readily attaches itself to and is 'taken over' by any nearby available female. Patas monkeys (Erythrocebus patas), on the other hand, are very jealous and exclusive mothers: other adults are not permitted access to the young, who thereby learn to avoid all but their own mothers; separation of mothers and infants in this case is especially traumatic to each.

In birds, parental behavior exhibited by both parents is as common, if not more so, than simple maternal behavior. This is especially so of those birds that establish mating pair-bonds that persist at least until the young are reared. Albatross parents, for example, share incubation duties and post-hatching feeding of the young. Indeed, Fisher (1968) reports that the food requirements of the youngster are so high that they can be maintained only by the combined efforts of both parents; a youngster that loses one of its parents prior to fledging has little likli-hood of surviving. Parent-young bonds in albatrosses, as in most birds, are quite exclusive: parents will tend only their own young and will drive others away (after the initial bond is formed, of course).

In other bird species where males gather harems and mating is promiscuous (or at least the mating pair bond has a short life), maternal behavior is more the rule. Chicken and turkey young are cared for exclusively by their mothers (either natural or adopted), and non-broody adults (those not exhibiting parental behavior), females as well as males, are as likely as not to kill any chicks they run across.

The Village weaver bird (Ploceus cucullatus) serves as a good example of a species wherein males essentially gather harems within their territories and have little to do with the young. As reported by Collias and Collias (1971), a male constructs an elaborately woven nest in his territory and then displays before the nest in an apparent effort to induce a female to 'adopt' the nest. If she does, mating then occurs and the male goes off to build another nest in quest of another female; if she doesn't, he tears down the nest and starts again. The female that accepts a nest thereafter has sole rights to it and the young she will rear in it; the male has nothing at all to do with the young.

In sharp contrast, however, is the interesting form that parental behavior has taken in the Mallee Fowl, a mound nester. Here, the male assumes full responsibility for constructing and maintaining the mound nest, and maintenance is a full time job extending over several months; the female appears only briefly to stock the nest with eggs and then disappears. Parental behavior in this species consists only of prehatching incubation, accomplished by manipulations of the mound by the male; after hatching, the young fend for themselves.

Among the reptiles, amphibia and fish, parental behavior tends to be virtually non-existent and approximates that of the non-social (asocial) invertebrates. About all that is involved is that the female lays her

eggs in some place where the young will have at least a fighting chance of survival prior to and after hatching. Female marine turtles, for example, bury their eggs in nests dug in the sand of various beaches and then leave. The young are left to fend for themselves, and the chances of survival are indeed slim: Carr (1973) estimates that only about one in a hundred make it to adulthood.

In some cases, however, quite elaborate parental behavior is typical of the species. Potential parents of various species of cichilid fish (Fam. Cichlidae), for example, build or dig elaborate nests in which to lay their eggs and rear the young until they are at least to the free-swimming stage; either one or both parents may be involved in the nest-building and/or young-guarding duties, depending upon the species.

An interesting, perhaps almost extreme, variant occurs in the mouth-breeding fishes of Africa. In the Mozambique mouthbreeder (Tilapia mossambica), the male digs a nest pit in the substrate. Following egg laying and fertilization in the nest pit, the female then scoops the fertilized eggs into her mouth where they hatch some two or three days later and the fry continue to develop for another ten days or so before emerging from her mouth for the first time. The mother continues to attend to the fry for several days after they emerge from her mouth: they return to her mouth at night and also at the slightest sign of danger. She facilitates the return, and probably even calls them to her, by assuming a particular "calling" posture, exhibiting a few sharp vibrations, and backing slowly. The return of the young to the mother's mouth gradually dissipates so that by some ten days after initial emergence, most young fish ignore "calls" by the mother and in fact avoid mouth-sized holes; this latter avoidance undoubedly is highly

adaptive.

Mouthbreeding in another species of Tilapia, the Blackchinned mouthbreeder (Tilapia melanotheron) is quite similar to that observed in Mozambique mouthbreeders with two significant differences. Whereas in the Mozambique it is usually the female (but occasionally the male) that broods the young, in the Blackchinned it is the reverse: the male (but occasionally the female) broods the young. Also, whereas in Mozambique the parent continues to attend to the young after they have emerged, Blackchinned young avoid the parent (and any adult) after the initial emergence; the Blackchinned youngster that enters its parents' mouth for the second time never again emerges intact from that or any other body opening.

Parental behavior is perhaps the dominant theme in the social insects, i.e., it is parental behavior that makes the social insects "social". Asocial forms display virtually no parental behavior; like the sea turtle described earlier, they do little more than lay their eggs in sites where the liklihood of survival of the young is enhanced, if ever so slightly. Such sites include proximity to a food source, or protection from the elements or from likely predators, or combinations thereof. The construction of an egg case, such as is characteristic of many asocial species, might be considered a step in the evolution of parental behavior. A more advanced form of parental behavior is illustrated by the digger wasp which lays its egg in a protective nest and provides it with a sufficient quantity of food to carry it through the larval stages. Mass provisioning (laying in a food store at the time the egg is laid) is characteristic of some of the more primitively social and solitary insects, such as carpenter bees, leaf-cutting bees, sting-

less bees, potter-wasps, and the like (Frost, 1942).

The more truly social insects, such as honeybees, ants and termites practice progressive provisioning of young. Here, parental behavior is very elaborate and is in fact carried out primarily by the older sisters rather than by the mother. In the honeybees, for example, the queen lays the eggs but the construction of the nest and tending of the eggs and larvae is the job of sterile female workers who are in fact sisters of the offspring. An excellent description of the workings of a honeybee colony, indeed of the evolution of social behavior in bees in general, is provided by Michener (1974). (An even broader look at insect societies and the social insects is available in a recent book by Wilson, 1974.)

2. Young-Parent Bonds. We have already discussed at length the establishment of young-to-parent bonds (see Imprinting and Associative Learning, pages 41-60), so a repetition here is unnecessary. It should be sufficient to recall that the young-to-parent bond is generally formed later than the parent-to-young bond, and the signals designed to elicit parental behavior are unique to care soliciting behaviors.

3. Mating-Pair Bonds. While bonds between adults of the same sex are certainly common in many species, bonds between breeding males and females are as extensive, perhaps even more so, as parental bonds. If parental behavior can be said to be indigenous to social behavior, mating behavior is even more pervasive. All social species have at least elements of parental behavior in their repertoire, but all sexually reproducing species, whether social or not, must mate. It should be noted that I do not consider the act of mating to be the sine qua non of

sociality, although in social species mating can be quite an elaborate social affair. In sexually reproducing asocial species, only minimal (if at all) bonds are established in the mating pair. Sea urchin sperm are released into the water and their union with an egg is almost (but not quite) fortuitous; the brief mating union of a male and female housefly cannot be considered much of a social interaction, even though by barest definition it actually is.

There does not seem to be any direct relationship between degree of sociality exhibited by a species and the complexity or persistence of mating-pair bonds. Instead, a wide variety of arrangements, from casual and promiscuous liaisons to lifelong mateships are observed; however, some generalizations across niche groupings may be possible, if not really useful. For example, in those species that establish "leks", such as the Uganda kob (Adenota kob), an African antelope, liaisons between males and females are very brief indeed: males establish themselves on small breeding territories from which other breeding males are excluded; females enter the territory and are mated after a brief courtship routine. Thereafter, she leaves the territory and the male is ready for the next visitor (Buechner, 1971). Equally promiscuous short-term liaisons are observed in a number of ground-living, grazing forms such as buffalo (Bison bison), turkeys (Meleagris gallopavo), impala (Aepyceros melampus) and the like where large mixed-sex groups are the rule.

Those herbivorous species that are organized in unisexual groups for much of the year also exhibit fairly casual mating-pair bonds. For example, throughout much of the year adult male Red deer (Cervus elaphus) are loosely organized in groups apart from the adult-female-plus-juveniles-

and-infants herds (Darling, 1938). During the breeding season, the males invade the female herds and establish "harems" for themselves if at all possible. Males vigorously compete for females to be included in their harems; attempts to maintain exclusive rights over their harems are not always completely successful. Thus pair bonding in Red deer is moderately casual and seems to rest more heavily on the fighting abilities of the male than on mutual choice by each partner. Elephants (Loxodonta africana) also often organize themselves into adult-female-plus-juveniles-and-infants herds, with adult males wandering separately as loners or in loosely organized groups. At various times, an adult male will join the female herd for a stay of a few days or weeks, during which time he will mate with whichever females happen to come into heat; indications are that a male joins the female-young herd only when one of the females is coming into heat, but some males have been observed to stay with the females for quite extended periods of time.

Mating-pair bonds are considerably more stable in species that establish territories, if only because the opportunities for casual liaisons are significantly decreased by the active defense of geographic boundaries. In fur seals, for example, males haul out on the beaches early in the breeding season and, with much squabbling, establish territories which they retain throughout the breeding season. Females join them in a week or two later, and there is there is the usual fierce squabbling among males as each attempts to corner as many females as possible in his territory. As in the Red deer, males attempt to exercise exclusive rights over their harems but transgressions are not uncommon (especially among the younger, less experienced males who are forced to establish more vulnerable territories on the edge of

the breeding beaches and are thereby subjected to harassment from other younger but less successful adult males).

More classic mating-pair bonds are characteristic of many of the perching songbirds, as exemplified by song sparrows (Nice, 1964). At the beginning of the breeding season, a male establishes a well defined geographic territory within which he meets all conspecific intruders. If the intruder is not a receptive female, he attacks it and drives if off; if the intruder proves by appropriate signals to be a receptive female, mutual courtship ensues and a mating-pair bond is established. The pair bond will generally remain intact throughout that breeding season or at least until the ensuing brood is fledged. Both the male and the female cooperate in the various chores associated with rearing the brood, such as feeding the young, maintaining the nest, and defending the territory from intruders. Since the territories are exclusive, i.e., there is little liklihood of encountering a non-agonistic strange conspecific in the territory, these birds are not burdened with elaborate discriminative or integrative capabilities: they tend to exhibit rather stereotyped behaviors based on simple "sign stimuli" signals. They are easily fooled by readily mimicked signals, which makes them especially vulnerable to nest parasitism by species such as cowbirds and cuckoos. Following the initial courtship that establishes the mating pair, post-copulatory and nest-greeting ceremonies are fairly simple.

Marine birds also tend to be characterized by mating-pair bonds, but the differences between them and the song birds are marked. For one thing, since space available for nesting seems to be at a premium, territories are often confined only to the nest and its immediate vicinity. Hence, nesting pairs are in continual and fairly close contact

with others and so capabilities for individual recognition must be high. This also means that post-copulatory and nest-relief ceremonies must be virtually as elaborate as pre-copulatory courtships, if only to enhance the retention of the characteristics of the appropriate partner. How elaborate the bond-establishing ceremonies are in Laysan albatrosses (Diomedia immutabalis) is described by Fisher (1968). Juveniles, two or three years old, engage in group courtship "dances" during the latter half of the breeding season; any and all seem invited to participate. By four or five years of age, individuals are concentrating more on paired courtship dances rather than group dances, and by five or six years of age the courtship dances are exclusively between now-established pairs, who will lay their first eggs the following year; the pair will remain intact throughout the lifetimes of the birds. Thus, courtship activities leading to eventual pairings start well before actual breeding occurs, and mating is for life. There is evidence also that mating pairs of mallard ducks are established in the fall, although the actual nesting and mating does not occur until the following spring.

Permanent lifetime, or at least long-lasting highly stable one-to-one mating pair bonds are not altogether too common in the animal world, but there are a fair number of species that exhibit such a trait and it may actually be more widespread than we realize. In addition to the albatrosses described above, other marine and shore birds (e.g., geese) might mate for life, and the same has been reported in foxes (fam. Canidae). Recently, Reese (1975) suggested that long-term stable bonds may be characteristic of some of the species of butterfly fish (Chaetodon spp.). More commonly observed, however, are quite stable bonds involving a male and a few, but not many, females operating as a family group; this type

of arrangement is frequently observed in large carnivores, such as lions (Felis leo) and wolves (Canis lupus), but is also observed in other species as well (e.g., Hamadrayas baboons, Papio hamadryas).

Mention must be made of temporary consort relationships established between a male and a female, usually centered around the period of heightened sexual receptivity of the female. DeVore and Washburn (1964) have repeatedly observed short-term consort relationships among Anubis baboons, which are otherwise somewhat promiscuous, and the same may be observed in mixed-sex herds of cattle (Bos taurus) and buffalo (Bison bison). In a temporary consort relationship, the pair remain in the proximate vicinity of each other and withdraw somewhat from the remainder of the group. Often, the male shields his consort from others, male and female alike. The consort relationship dissipates when the female is no longer sexually receptive, which may be in a matter of a very few days.

In summary, then, while parent-young and young-parent bonds are almost diagnostic for social species, mating-pair bonds are not; they run the gamut from fleeting brief liaisons characteristic of asocial species to moderately stable but fixed-term bonds to long-term or even permanent one-to-one bonds. About all that can be said as a generalization is that if the mating-pair bond is more than a brief encounter, then we are dealing with a social species.

4. Monosexual Pair Bonds. Bonds between adult members of the same sex are not uncommon throughout the animal kindgom, but the basis for such non-mating 'friendship' bonds is not always understood. Among various primate groups, there have been repeated observations of certain individuals of either sex showing much greater affinities for each other

than for other members of the group. Watts and Stokes (1971) describe a related situation in turkeys on the Weller Wildlife refuge in Oaklahoma. Here, groups of two or three males cooperate in maintaining and guarding a harem of females within a territory; however, only one of the males ever mates with the females, and the supernumery males seem to function primarily as a back-up reserve.

We have already mentioned above the all-male group arrangements of Red deer outside of the breeding season, and of elephants both in and out of whatever breeding season there is. Such groups of surplus males are not uncommon in harem-establishing species: there simply are more males than are needed to maintain the species. Southwick suggests (1972) that the exclusion of males from the breeding colony may be related to the availability of resources: in the region of Jodhpur, India, at the edge of the great Rajasthan desert, where conditions are sparse, the Hanaumon langur (Presbytis entellis) group consists of a single male and a coterie of females, juveniles and infants; all other adult males are relegated to loosely organized all-male troops living elsewhere, with only occasional interactions between the all-male and the breeding troops (Mohnot, 1971). Some surplus males move about as loners, but little is known about them since they wander extensively and are difficult to study. In contrast, in the more lush regions of South India, the same species exhibits multi-male mixed species groups; all-male troops are non-existent.

Differences in the strengths of social bonds within unisexual groups is well described by Darling (1937). During the breeding season, the all-male herd invades and permeates the female-young herd making in effect an overall mixed-sex group. However, if one were to suddenly startle the herd, the female-young group runs off as a unit while the males scatter

in all directions. Apparently, the female-young herd maintains its integrity as a group despite the invasion of the males, while the male group has little real internal integrity.

5. Juvenile Peer Bonds. Peer bonds are especially prevalent among juveniles of roughly equal ages. Among the mammals, pre-weaning sibling peer bonds are evidenced in those species that produce litters of young, but where young are produced singly, then peer bonds tend to be most firmly established after weaning. Juvenile peer bonds and peer groups are much characterized by play activity, especially in those species (such as the various primates) where play is prominent and well recognized. DeVore noted (e.g., 1961) that peer bonds established by juvenile Anubis baboons are formed during the maturation period and determine the relationships among the subsequent adults; we have observed the same in cattle, and suspect that such is the case among many social species that live in relatively closed groups (i.e., where movement of individuals from group to group is somewhat limited).

Group Bonds

1. Individual to Group. In many social species, individuals not only form long and short term associations with other individuals, but they form associations (or identify) with the group as well. In fact, a social group such as a troop of baboons or a herd of elephants exists as a complex of interwoven bonds between and among individuals, and there are hierarchies of bonds ranging from the very intimate parent-young bond to the much more loosely defined identity with the group.

That identification with a group is real is evidenced in several ways. We have described the cohesiveness of the female-young red deer

group as contrasted to the looseness of the male group. In a similar vein, there are many descriptions of "outsiders" being treated severely by members of established groups of primates, sheep, chickens and turkeys: the outsider, or outcast, must gradually and carefully insinuate itself into the group before it is accepted as a group member, an incast. Southwick (1972) reports that in Rhesus monkeys, outsider adult males are practically never, if ever, accepted into an established group. Adult females have only a slightly greater chance of being accepted and juveniles still greater, but infants are invariably readily accepted and adopted by one of the group members.

Among the highly social insects, outsiders are simply not tolerated at all. The honeybee that inadvertently enters the wrong hive usually does not live to repeat the error. Apparently, members of the same group recognize each other on the basis of a common chemical label peculiar only to that hive; anyone with a different or the wrong label is immediately killed. Parasitic species, such as wax moths, are able to mimic the chemical label and thereby freely enter (and subsequently destroy) the hive.

2. Group to Group. There are a number of studies reporting on group-group relationships, especially among the primates. Carpenter's early 1934 study of Howler monkeys (Alouatta palliata)provided a template for later studies of within- and between-group interactions in primates. He found that the Howlers were organized into cohesive groups, with each group operating in a reasonably well defined geographic area. When two adjoining groups found themselves near each other at a border area, the males of each group would "threaten" the members of the other group by means of raucous howling. Thus, territorial defense was a cooperative

group effort.

Essentially similar scenes have been reported in other primate species by many other workers, except that group to group interactions are not necessarily hostile. DeVore (see/ Devore and Hall, 1965; Hall and Devore,1965) noted that on a number of occasions, neighboring troops of Anubis baboons would come together and intermingle peacefully for a few days before going off on their separate ways. Similar observations have been reported for troops of Rhesus monkeys on Cayo Santiago Island off Puerto Rico and in Black-faced vervets (Ceropithecus aethiops) in East Africa. Juveniles frequently take especial advantage of such peaceful interminglings by coalescing play groups so that what appears to be a grand time is had be all.

Not all such group meetings are so peaceful. Although sometimes the Rhesus troops on Cayo Santiago peacefully intermingle when their paths cross, more often than not certain groups tend to avoid others so that their paths do not cross. The several distinct troops on Cayo Santiago have overlapping home ranges and seem to be arranged in a hierarchial order much like that reported for individuals (see Section II, Hierarchies, pages 86-104). Thus, troop A and all its members are dominant over troop B and all its members, and so on through troops C, D, E, and F. In the course of its wanderings and at the food hoppers, members of troop C, for example, do not hesitate to displace members of troops D, E, or F, but readily yield to their counterparts in troops A or B (Koford, 1965; Issakian, personal communication). In a more open situation where much more space is available, the home ranges of the several troops would not be likely to overlap extensively and so a hierarchial arrangement of troops would be less evident, if it exists at all in the natural state.

3. Interspecific Groups. There are a number of reports of interspecific associations but little real evidence that the interactions between the different species are truly social. Cattle egrets (Bubulcus ibis) are often found around, and are tolerated by, various large herbivores; they apparently thrive on the insects stirred up by the grazing activities of the larger animals. While such a relationship is directly beneficial to the egret, it confers at best only peripheral and only incidental, if any, benefit to the herbivore (in terms of perhaps reducing the insect load on these animals). More obvious mutual benefits are apparent in other interspecific relationships, such as that between the water buffalo (Syncerus caffer) and the buffalo weaver (Bulbalornis albirostris). Here, the little bird is well tolerated by the massive buffalo: it searches for and eats various insects and insect larvae on the body of its host; the weaver bird gets a meal and the buffalo is relieved of some of its ectoparasitic burden. Some interspecific signalling must be involved, since the buffalo does not permit just any old bird species to feed off its body, particularly around such delicate areas as its eyes, nostrils and lips.

Somewhat looser interspecific relationships are frequently observed in species whose geographic niches overlap somewhat and who do not present a threat to each other or at least are not in major competition with each other. Thus, baboon troops in Africa often graze side by side with impala or gazelle herds, and mixed herds of various herbivore species are not uncommon. In the fall and winter months, huge mixed-species flocks of birds, chiefly starlings (Sturnus vulgaris), grackles (Cassidix mexicanus) and redwing blackbirds (Agelaius phoeniceus), numbering perhaps in the millions of individuals can be observed returning every evening to

their roosts in the coastal marshes of the Northeastern United States.

Indications are that in most or all of the commonly observed mixed-species groups, some rudimentary interspecific communication may be possible: at the very least, they seem responsive to each other's alarm signals a' thereby derive benefit from group associations. Indeed, such interspecific associations might prove to be a most effective strategy in defense against predators, since not only can a group capitalize upon another species' often unique perceptual talents, but many more predator detectors are called into play without the direct expense of increased intraspecific competition. Thus a group of 50 baboons associated with 50 gazelles would likely be under less internal stress and suffer less outside threat than a group of 100 baboons operating alone. The concept that species associations might be more beneficial to one species, in that the other species may be more acceptable to a predator, necessitates a reciprocal benefit (perhaps with a different predator species) if the association is to be sustained.

A more intimate interspecific relationship is evident between cleaner fish of various species and the fish they groom. Typically, a cleaner wrasse (Labroides spp.) is brightly colored and establishes itself in a well defined and prominent geographic location. It approaches much larger fish that enter its "territory" and after appropriate stimulation that induces the larger fish to "stand" for "grooming", "grazes" on the body surface of the larger fish which, incidentlv, postures accordingly which maximizes the coverage and effectiveness of the cleaner's operations (Losey, personal communication). There are indications that cleaners even build up a clientelle of fish that repeatedly and periodically return to the same station for grooming, and the analogue to our local hairdresser

shop is not so far fetched (Losey, 1975).

That such interspecific associations border on sociality cannot be disputed. Certainly, many of the criteria for sociality are met: cooperation, mutual advantage, adaptiveness, at least a minimal degree of communication. What is lacking is any evidence for the establishment of specific bonds between individuals, which therefore eliminates the possibility of forming cohesive social groups that in turn enhance the survival probabilities of the progeny. I prefer instead to consider such inter-specific interdependencies (and there are many examples of symbiotic relationships between species) as quasi-social rather than truly social relationships. Quasi-social relationships contain some or even many of the elements of truly social relationships but they lack one important element: the direct enhancement of progeny survival by means of parental behaviors and (usually) parent-young bonds.

Interspecific Socialization: A Special Case

Are there, then, any examples of true socializations between members of different species? I believe the answer is "yes, but . . ." Yes, but they generally occur only in particularly contrived laboratory situations or they sometimes inadvertantly (or even deliberately) occur with our domestic animals. The orphaned lamb that is adopted by the farmer and thereby becomes human imprinted may be an example of an interspecific socialization. Laboratory manipulations, such as occur in imprinting experiments, also yield examples of true interspecific socializations. The bonds in these cases are necessarily weak unless the communication link between the imprinted animal and its adopted parent species is broadened beyond the mere basic essentials.

To illustrate the above points, let me offer some basically anecdotal evidence; hard, non-anecdotal evidence is not yet available. In the course of working with any of a number of animal species, including especially cows, chickens, turkeys and Japanese quail, one fact emerges especially clearly: the relationships between the study animals and their human handlers is strictly along interspecific lines, with the human species generally dominant. Most of the animals are somewhat wary in the presence of humans and maintain a comfortable distance between themselves and nearby people. Some individuals may become "pets" and, by the process of familiarization reinforced by rewards and reinforcements, thereby maintain significantly lesser distances between themselves and humans; much of their human-oriented behaviors take the form of care-soliciting behavior. An occasional other individual may, under certain circumstances (as when its young are threatened), attack nearby humans; such attacks are generally part of its anti-predator repertoire. The relationship of one species dominant over another persists throughout.

A very different picture emerges in the few instances where we have reared human-imprinted turkeys that were permitted to attain higher dominance rank in the turkey-human relationship. This is rather difficult to accomplish since it is very easy for us to dominate a turkey, let alone a human-imprinted turkey, by ignoring its various agonistic signals and simply overwhelming it. However, with diligent care to insure that its signals were not ignored, the desired goal was attained and we were able to compare the behaviors of dominant turkeys to the more commonly available subordinate (with respect to humans) human-imprinted turkeys avoid more dominant turkeys, but the dominant human-imprinted turkeys showed no hesitation in approaching humans whenever the occasion

warranted, just as ominant turkey-imprinted turkeys do not avoid subordinates. When approached by a dominant human-imprinted turkey, our role was to get out of the way; if we did not move fast enough, the turkey would emit threat signals or occasional pecks to help us on our way. On one occasion we slipped: in getting out of the turkey's way, it inadvertantly got kicked; dominance was immediately reversed and it took especial effort to re-reverse the dominance. Thus, we were clearly treated as another turkey, so long as we played the game according to turkey rules, and were thereby able to enter into the social system as equals: true interspecific sociality.

Disruption of Social Bonds

By now it should be obvious that social bonds are not inherently permanent, and that some bonds are more readily disrupted than others. Let us look first at some disruptions that are so commonplace as to be predictable and expected, and then at some of the factors leading to temporary or permanent disruptions of social bonds.

Types of Disruptions

1. Substitution Breaks. The substitution of one partner for another, for whatever reason, is so commonplace as to warrant little attention. Such substitutions occur routinely in adult and juvenile peer bonds and, in many species, in mating-pair bonds. The routineness with which such substitutions occur testifies to the ephemeral nature of many social bonds; little more is involved than simple associative learning acquisition, retention and extinction.

2. Seasonal Breaks. In at least some long-term stable mating-pair bond associations, the bond seems to be dissipated, at least temporarily, during the non-breeding season. In permanently mated pairs of albatrosses, males return to the nesting sites at the beginning of the breeding season, a week or two earlier than the females; they also leave the nesting area separately at the end of the breeding season. Since albatrosses observed at sea tend to be loners, the evidence seems to point to the fact that the pair bond is not sustained outside of the breeding season, and thus the bond is disrupted annually.

Little is known about other species that might possibly establish long-term mating-pair bonds but do not stay together all year (e.g., other marine birds, some of the song birds) because repeated observations of individuals at sea or in huge winter flock aggregations are extremely difficult to make.

3. Parent-Young Breaks. Bonds between parents and young, so firmly established and so much the foundation of social behavior, normally wane or are permanently disrupted in due course. In most species the break occurs gradually as the young develop and is completed by the time the young reach maturity; the newly mature individuals lose all contact with their parents as they assume roles that call for the establishment of new social relationships. Permanent breaks are especially characteristic of those situations where geographic despersion is the rule: young adults move out to new areas or force their parents to move out, such as is typefied in wild rats (Rattus norvegicus). However, in groups that maintain territorial or home range cohesiveness over time (such as wolves or elephants) so that several generations may be represented in the group at any one time, parent-young bonds might possibly persist throughout the

lifetimes of the individuals involved. Such may be the basis of organization of female-young elephant or deer herds. The persistent bond is of course not anywhere near as tight as when the youngster was still an infant, but some traces of parental protection continue to show in the form of deference to lead animals (who, in the case of deer and elephants, tend to be the older females).

An instance of the remnant of parental behavior was brought home to me a few years ago, on a visit to the free-ranging rhesus colonies on Cayo Santiago Island off the coast of Puerto Rico. A group of us were sitting on the ground discussing one of the troops that had joined us and were sitting all around us. We would occasionally toss food pellets to the troop to watch the interactions among troop members. Closest to us was the dominant male, who was backed up by other adult males and a few older juveniles. Behind the males were females and younger juveniles; furtherest from us were the females with infants and a few non-descript low-ranking old animals. Everything seemed quite peaceful until one of us accidently made a hand movement that was reacted to as a threat by the dominant male, who issued an alarm bark and leaped back. All the others immediately responded in the same fashion and there was a general and confused scurry away from us. One individual, however, was different: an old low-ranking female from the periphery ran towards us with threatening gestures. In a very short time the excitement subsided and the monkeys resumed their pre-threat places: the males came to the forefront and the old female returned to the periphery. We were not too surprised to discover from our host that the old female that threatened us while the dominant male and all the others were retreating was in fact the mother of the dominant male.

Factors Leading To Disruptions

Disruptions of social bonds may be traced to any one of several key factors. Competition for available resources seems to be one of them and is perhaps the basis of the break between the parent and its young. As the older youngster is replaced by a younger sibling, the benefits it derives from the parent become increasingly more difficult to come by and the individual is eventually forced out completely. In wild rats and in many other species, competition for available resources forces continual branching out of the group: newer individuals simply move out. When there is no longer any place to move to, or when moving out becomes increasingly difficult, then weaker individuals (newer or older) are forced out. These emigration moves necessitate the disruptions of old social bonds and the establishment of new ones. Other more regular seasonal migratory movements, exemplified by a number of species, may also involve shufflings in social bonds since often great numbers of individuals are involved and smaller social units are merged into the mass. Sometimes migratory waves consist of age and sex-specific groups, which surely must at least temporarily disrupt premigratory social units.

Another key factor in the disruption (and of course establishment) of social bonds is the physiological state of the individual. The adult whose gonads regress because of seasonal changes is no longer going to form or retain mating-pair bonds. The parent bird undergoes changes in endocrinological balance as the young mature, and such changes lead to the dissipation of parental behavior and the parent-young bond. Thus, physiological state governs responsiveness to environmental stimuli: in one state, a set of cues may elicit courtship or parental behaviors and attendant bonding; in another state, the same cues could elicit completely different behaviors or might be ignored altogether.

III. STRUCTURES OF SOCIAL GROUPS

Having considered sociality in general and examined its basic unit, the social bond, in terms of its formation, maintenance and disruption, we may now turn to an examination of the structures of some social groups. As we have already discovered many social groups are cohesive entities with social boundaries: members of a group are distinct from non-members and individuals assume distinctive roles which, when properly integrated, make for the proper and smooth functioning of the group. It is perhaps the phenomenon of roles that distinguishes between a cohesive group and a loose aggregation.

In aggregations consisting of members of asocial species or even those made /up members of social species, each individual plays the same role as the others; bonds are not formed, since none derives any particular benefit from the others except perhaps in the most primitive sense discussed earlier (see pages 22-23). Thus we see large feeding aggregations in social and asocial species or aggregations around a water hole or some other concentrated environmental resource. In many senses, the loosely knit all-male elephant or Red deer herds or the surplus-male troops of Hanuman langurs represents more an aggregation than a social group. One might say the same about many incidental or accidental clusters of humans around some environmental feature: subway riders densely packed in a car during "rush hour" are probably more of an aggregate than a social group.

This does not mean that there cannot be social units within an aggregation; indeed, there can: aggregations often consist of clusters of social units as well as clusters of individuals. Family units, with all the implicit social bondings contained therein, or simple peer bonds,

may be represented in our packed subway car or in the aggregation around the water hole. Still, the overall complex is an aggregation since it lacks general organization and the definitions of roles that make for organization.

Family Unit Packs

Just as parental behavior is fundamental to social behavior, it follows then that the family unit is basic to the structure of social groups, and so it is in most cases. (The exceptions might be those species, such as the parasitic birds, that have evolved strikingly different ways of having their progeny reared.) The family unit consists of a mated pair and its progeny, or even more simply (and especially in promiscuous species) a parent (usually female) and its young. Let us consider first the family unit that consists of both parents (a mated pair) and their young; later, we shall examine the type of structures that stem from single parent units.

Mated pairs that together rear families tend to be stable (at least throughout that breeding season) and more or less territorial. One or both parents participate in guarding the territorial boundaries and the nest site, although (as we have seen with the marine birds) the territory and the nest site may be one and the same. Relationships between the parents may be such that they have equal rights and equal responsibilities, so that there is a truly equal partnership, or it may be (and more commonly) that the role each plays supplements rather than overlaps the others'. In either case, the dominance of one over the other does not enter the picture since there is little if any competitive interactions between the two. Nevertheless, either or both parents dominate the young, since the

parents control the environmental resources. Needless to say, dominance in most cases is quite benign.

Rarely does a family unit exist totally isolated from other nearby conspecifics, including other family units, and the relationships between family units is essentially that of between equals. Territorial transgressions occasionally happen and for the most part are successfully repulsed: each unit is dominant in its own territory and subordinate in others. The integrity of the territory and therefore of the family unit is maintained.

While song-bird family units and territories break up at the end of the breeding season, some other family units maintain integrity throughout the year. In such cases, the strictly defined and strongly defended territories characteristic of seasonal breeders give way to more loosely defined group home range areas where two neighboring groups are not likely to be in the same place at the same time. At the same time, the individual families coalesce into one or a few extended families, or in at least one case, (the Hamadryas baboons) form loose aggregates of family units. (In the Hamadryas baboons, "troops" consist of a number of "units" and each unit consists in general of a male, one or two females, and their young; troops are only loosely organized, in that units freely join or leave the troop; each unit enjoys more or less equal status with all other units.)

Stable year-round family units are exemplified by wolf packs and various other carnivores. The pack consists of one or at most a few family lines and may contain two or three generations at any one time. Relationships between individuals is considerably more complex than the simple song bird families described above. Here, a dominant male may extend control over other males and several females, who in turn exercise control over the young. In addition, the other males and females in the pack

(many of whom may be inter-related) may exercise varying degrees of control over each other so that some sort of hierarchy may emerge. In a group as well defined and cohesive as a pack, specific roles, often gender related, are apparent: dominant male, peripheral male, dominant female, subordinate females, juvenile, and the like. With each role comes certain responsibilities, such as procurement of food and defense against intruders, and the net result is a well functioning pack that is successful in producing healthy progeny.

Hierarchies

Where mated pairs do not persist and therefore the rearing of the young falls to only one parent, most commonly it is the female the assumes such a role (but note exceptions discussed previously, cf. page 13). Attendance to parental duties, however, means some degree of sacrifice in the prosecution of other important duties, such as defense against predator. Thus, female-young social units are nearly always subsumed in larger groupings where some measure of protection is available from attendant free-roaming males or from the simple expedient of group size. Thus, herds, flocks, and troops are characterized by structures built around the basic female-young unit. Again, roles are sharply defined, often gender-related, and different roles may imply responsibilities for different functions: defense, protection of young, leadership in movements, and the like. With the exception of mothers feeding young (or at least helping the young to find food), for the most part the acquisition of food and provender is an individual prerogative in herding, flocking, and trooping species.

The general organizational principle of herds, flocks and troops is dominance-subordination as expressed in some sort of a hierarchial social structure. When two conspecific individuals compete for a limited resource and invoke agonistic behaviors to influence the resolution of the competition, one will "win" and the other will "lose" ("stand-offs" sometimes occur but are not all that common.) If a second confrontation between the same two individuals occurs, but this time the previous loser defers to the previous winner, then a dominance-subordination relationship has been established between the two animals. So long as the loser continues to defer to the winner, further overt conflict is obviated; simple threats replace outright combat, and each is spared the possibility of grievious, perhaps even fatal, bodily harm. Note that the active principle sustaining the relationship is subordination rather than dominance: conflict is reduced in intensity, if not avoided outright, when one defers to the other rather than when one attacks the other. When the subordinate individual decides to no longer be subordinate, it must challenge and vanquish the dominant who usually does not relinquish the position very readily: the burden of action rests upon the shoulders of the subordinate.

Individuals in finite sized defined groups frequently have dominance-subordination relationships with all other members of the group, and the relationships can often be arranged in a hierarchial fashion so that one individual is dominant over all the others in the group, another is dominant over all except the first, a third is dominant over all except the first two, and so forth. More properly put, one individual defers to all other members of the group, another defers to all except that one, a third defers to all except those two, and so forth until finally one individual, the dominant, defers to none. Dominance hierarchies have been studied

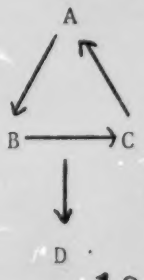
extensively by many researchers, chief among which were W. C. Allee and his students, after the initial description of hierarchies in chickens by Schjelderup-Ebbe (1922). In addition to domesticated chickens, hierarchial social structures have been reported in such diverse animal groups as primates, cattle, cats, rodents, canaries, tortoises, sunfish, crayfish and even wasps, among others (Schein, 1975). The phenomenon is indeed widespread and elements have been invoked in descriptions of social structures of innumberable species, including humans; phrases such as "rank order" and "peck order" have become well integrated into our common parlance. Other synonyms of dominance hierarchies include social rank, social hierarchy, hook or bunt order (in cattle), butt order (in sheep and goats), and social order.

The classical picture of a straight-line dominance hierarchy shows all members of the group arranged in a perfect row (Figure 10). The most

Fig. 10. A straight-line dominance hierarchy. A → B → C → D → E

dominant animal, A (alpha), defers to none; the next in line, B (beta), defers only to A; and so on down the line to E (omega), who defers to all. But dominance orders are rarely so neat and simple, especially if more than a mere handful of animals is involved. Triangles, where A dominates B, B dominates C and C dominates A (Figure 11) are common occurrences and

Fig. 11. A triangular dominance order.



of course can be much more elaborate. Ranks can also be shared, especially lower ranks (or at least we, the observer, cannot determine the relationship between a pair of animals). Several different hierarchial arrangements are depicted in Figure 12; other arrangements are of course possible, but the basic dominance subordination principle is not violated. The relationship shown in Figure 12(d) represents an arrangement we found in laboratory mice: one individual, A, clearly dominated all the others but relationships among the others were notoriously peaceful. However, if A were removed, one of the others would immediately assume the dominant position and would tyrannize its former peaceful companions just as did its predecessor (Clark and Schein, 1966).

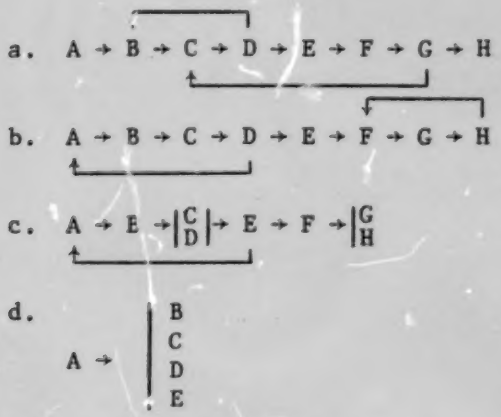


Fig. 12. Examples of several different dominance orders.

Factors Determining Rank Position

The position of individuals in the hierarchy of dominance is determined by a dynamic complex of factors operating when the group first comes together and continuing to operate, but perhaps in a different balance, as relationships within the group stabilize. Randomly occurring chance events may be important in conferring temporary advantages or disadvantages at first meeting but are far less important after relationships

are well established. Let us examine some of the phenomenological factors most commonly associated with rank position; detailed studies of most of these factors have been assembled together by Schein (1975).

1. Seniority. In a stable group with few significant advantages to lose by accepting subordinate status, rank position is highly correlated with seniority. Since recruitment in such stable groups tends to be from birth, as in a closed herd, the senior member of the group is also the oldest surviving member of the group. However, in a few instances where we have been able to introduce young outsiders to an otherwise closed herd of dairy cows, we found that age per se was not as important as other factors, thus leaving seniority to stand by itself. The senior animal may have long passed its peak of physical condition and may in fact be somewhat decrepid and infirm, but in a closed stable group (such as in dairy cows) it will retain dominant status until it dies.

2. Strength. In a less stable group where there may be an influx of outsiders for one reason or another, or where significant advantages accrue to the dominant individual, the factor of strength is important in determining the outcome of initial (and to a lesser extent, subsequent) interactions. The strength factor includes purely physical features such as size, weight, state of physiological well being, locomotor abilities, and coordination, to name but a few. In lower vertebrates, weight and size are highly correlated with rank but in higher vertebrates the correlation is not always so clearcut. In other words, all things being equal, the stronger animal will win; but all things are usually not equal, especially in the less stereotyped forms.

3. Experience. Experience encompasses the development of fighting skills, abilities and agility that stem from repeated exposure to agonistic

situations; it could also encompass the development of evasive and avoidance patterns that are related to submission rather than dominance. Winning begets winners and losing begets losers: an animal with an immediate past history of winning is likely to win in its next encounter. An old laboratory routine that illustrates this point very well is to stage a set of fights between pairs of chickens. In the next set of fights, winners from the previous set are paired against losers from that set. Almost invariably, those that won in the first set will win again. By the time three or four such "sets" are conducted, the "winners" hardly wait to challenge but simply attack, while the "losers" do not wait for the attack but simply flee. Then, when two "winners" are paired against each other, each immediately attacks and the level of interaction is fierce. On the other hand, if two "losers" are pitted against each other, both avoid and flee at the outset; the first that discovers that the other is fleeing reverses direction and now chases and attacks. With a few carefully staged bouts, the once "loser" can now be converted into a "winner".

4. Sex. As mentioned earlier, males tend to be dominant over females in many species. Chances are that this relationship is based as much on strength (weight, size) as on sex per se: in many species, males are larger and heavier than females. Still, on an equal weight-size basis, male chickens, turkeys and cattle are dominant over females so there may be a hormonal-behavioral basis to the sex distinction. On the other hand, size, not sex, is correlated with rank position in crayfish; in Japanese macaques (Macaca fuscata) , sex is not related to rank position (Eaton, peronal communication).

5. Genetics. Some varieties or genetic strains are virtually always dominant over others. Among turkey varieties (which are genetic strains),

Blacks always dominate Bronzes even though the Bronzes are on the average heavier and bigger birds. In laboratory mice, the C57Bl strain developed at the Bar Harbor laboratories is highly pugnacious and quick to attack; it easily dominates mice of other strains, and in fact often kills the subordinate. Guhl, Craig and Mueller (1960) were able to develop strains of "winners" and "losers" in White Leghorn chickens within only four generations of selection for winning or losing. It is interesting to note (Figure 13) that

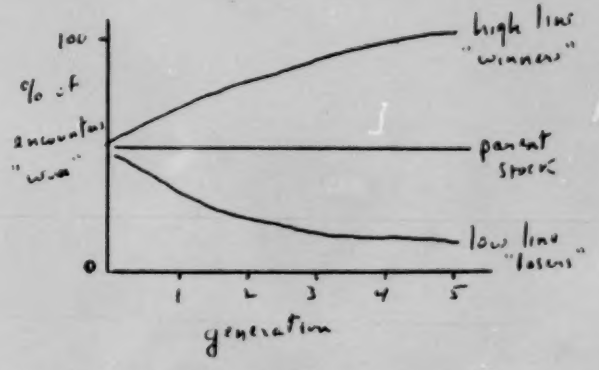


Fig. 13. The development of "winners" and "losers" in chickens.

despite continued selection, he was unable to increase the difference between the two strains beyond the point reached by the fourth or fifth generation. However, each strain remained significantly different from each other and from the randomly bred parent stock.

Just how selection influences the outcome of agonistic interactions is not altogether too clear. One would suspect that selecting for pugnaciousness and readiness to attack, as apparently is the case in the C57Bl mice, would lead to initial advantages in encounters with more docile strains. Certainly, the one that initiates the attack, the aggressor, has a momentary advantage which frequently is converted into success. However, initiation by itself is not enough: the aggressor must be prepared to sustain the attack if the need arises. C57Bl mice do sustain the attack, and encounters between two C57Bl mice often end only with the

death of one of them. Similarly, Game cocks, which are heavily selected for combative abilities, fight to the death. Siegel (pers. comm.) suggests that attack and submission may be separable genetic traits, that in fact selection in fighting Game birds has been against submission as well as for attack; thus, the initial attack is sustained.

An interesting, but perhaps not too surprising phenomenon that has been observed in wild rats is that the offspring of dominant animals tend to also be dominant. In Calhoun's early rat enclosures, the dominant animals established themselves around the food sources and subordinates had to virtually run an obstacle course in order to reach feed and water. Consequently, nutritional levels were markedly different among the rats, with higher order animals and their offspring being significantly healthier than the lower order animals and their offspring. Small wonder then that the offspring of dominant parents would in turn become dominant over the others.

Still, we should not be quick to discount the possibility of a genetic basis for the inheritance of dominance. We mentioned earlier that a hierarchial order was evident within and between the Rhesus monkey troops on Cayo Santiago Island. It turns out that dominance begets dominance in the monkeys as well as the rats: the young of higher order females attain higher social rank at maturity than do the progeny of lower ranking females. In this case, however, differences in nutritional status and in general health may not exist or at least are not apparent: food and other necessities are widely and adequately distributed around the island. Perhaps the initial advantage over peers gained by a pair association (see below) is sustained as the animals in the peer groups mature. Or perhaps dominance is transmitted from generation to generation

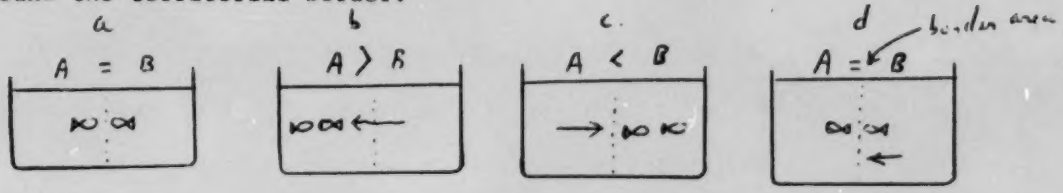
as a natural consequence of transmitting characteristics leading to superior size, strength and agility. In any event, whether "cultural" or "biological", dominance is often passed from one generation to the next.

6. Pair Associations. In consort relationships, the rank of each member of the pair is that of the one with higher status. Thus, pair associations are advantageous to lower-order individuals in that their status is elevated so long as the relationship is maintained. Once the relationship is broken, however, the consort generally reverts to its originally lower rank position in fairly short order. The phenomenon of assuming the rank of the higher-order member of a pair has curious effects: a low order female that establishes a consort relationship with a dominant male gains temporary dominance over other males who ordinarily would have quickly put her in her place. Similarly an infant in close association with its mother assumes the rank of the mother and is thereby dominant over older juveniles who no longer enjoy the protection and status of their mothers; thus, the younger infants have an initial social advantage over their older siblings, but this advantage wanes as the parent-young bond deteriorates in favor of another infant on the way.

7. Familiarity. An animal fights best on its own terrain; those that invade and are thereby less familiar with the terrain are at a distinct disadvantage which may be great enough to tip the balance against them. Thus, territorial animals are able to repel intruders for which they would be no match in a more neutral setting. In an early series of studies, Tinbergen (1953) found that the fighting success of cichlid fish (Gasterosteus aculeatus) was inversely related to the distance each fish was from center of its territory. When placed in an aquarium, each fish established a territory that was limited only by the extent of its neighbor's territory.

Fish with adjoining territories patrolled the borders, and interactions at the border were inconclusive: the chances of winning equalled the chances of losing (Figure 14a). However, in the event of an intrusion, the deeper one fish penetrated the other's territory, the greater were its chances of losing an interaction (Figure 14b). As the intruder was

Fig. 14. Oscillation of fish around the territorial border.



chased back into its own territory (Figure 14c), the probability of its winning an encounter increased; it turned on its neighbor and chased it back towards the neighbor's territory (Figure 14d). Thus, interactions and chases oscillated back and forth and so defined the border area.

8. Hormones. The general physiological state of the animal undoubtedly affects its combative abilities and therefore its position in anything but the most stable heirarchies. Sick and infirm individuals are quickly reduced to low status unless they find protection in a pair association. Hormones in general affect rank position indirectly, in the sense that an animal with a malfunctioning thyroid gland is not operating at peak efficiency and therefore is at a disadvantage in dealing with others. However, certain hormones, and especially the male sex hormones (the androgens) have been demonstrated to be particularly significant with respect to combative abilities and rank position.

Given an established group of roosters, if one of them is castrated it quickly drops to the bottom of the rank order. It can regain its former position, however, if androgen treatment (i.e., periodic injections)

is administered; it will retain that position so long as the treatment is continued, and drop again if the treatment is discontinued. If one hen in an established group is injected with male sex hormones, she rises in the rank order and stays up so long as the injections are continued; she reverts to her former rank when the injections are discontinued. Of course, the picture is not quite as simple as presented here: the factor of "experience", among others, dampens abrupt shifts in social rank. Thus, if the beta hen were injected with male sex hormones, it probably would achieve alpha status in short order; however, if the omega animal were injected, it would take considerably longer for it to break the habit of submitting and start moving up the social ladder. Once it achieves alpha status, the experience of winning (and its colleagues' losing experiences) may well keep it in a high position long after the hormone therapy has been discontinued.

The relationship between androgen levels and fighting abilities and pugnaciousness has been well established in many vertebrate species. However, other hormones may also be involved in some species or in certain contexts: Davis (1957) found that social rank in male starlings (Sturnus vulgaris) was related more to levels of adrenal corticoids than to male sex hormone levels. Further, while not necessarily having any long-term effect on rank position, it is well recognized that some of the hormones involved in parental behavior significantly affect levels of pugnaciousness: a moderately low ranking female will vigorously defend her young against attacks or encroachments by higher ranking conspecifics, male and female alike, as well as by predators.

9. Age. Apart from considerations of seniority, age is an important factor in terms of stage of maturation. In most social species, the

very young and immature animals are not part of the rank organization of the group. If anything, they rank below the lowest individual in the hierarchy and there is little if any evidence of ranks among the peers in immature groups: groups of chicks, ducklings, lambs, and calves are not hierarchially organized. Even in many primate groups, where infants are blessed with the ranks of their mothers at the outset (see Pair Associations, above), they lose such status as they move out into young juvenile peer groups which are essentially unranked.

However, as the youngsters mature, casual and play peer-associations harden into rank positions among themselves and they enter into the adult community, usually at the bottom of the hierarchy. Guhl (1962) found that hierarchies in chickens developed at about 6-8 weeks of age, coincident with sexual maturity, but we have observed that dominance-subordination in dairy cows is well established by 6 months of age, long before puberty. Similarly, in primates, hierarchial positions seem to be established prior to maturation, but just how much prior is not known.

Hierarchy and Levels of Interaction

We have already pointed out that the introduction of several chickens, strangers to each other, into a neutral pen would generally be followed by intensive agonistic interactions among the birds, but that the level of interactions would quickly decrease as each bird established its relationship to each of the others (see page 31 and Exercise 8, page 192). Therefore, low-intensity agonistic interactions prevail as the group goes about its normal routine activities.

It is important to note that the development of a social structure from a previously unorganized aggregate, although initially marked by

intensive conflict, is correlated with a reduction in the level of conflict in the group. Once relationships between individuals are recognized and accepted, there is no need to continue high level potentially damaging interaction; reinforcement of status positions and resolution of conflicts can be accomplished by actions of much lower intensity. Thus, physical combat might be used initially to establish a relationship, but simple threats can subsequently sustain it. The decreased probabilities of overt physical damage undoubtedly has adaptive significance even though low ranking individuals may be (at least temporarily) removed from the breeding pool.

In large hierarchially organized groups, the probability of an individual interacting with any other member of the group is not purely a matter of chance. We have found that in dairy cows, individuals were more likely to interact with closely ranked neighbors than with others more distantly removed on the rank scale (Schein and Fohrman, 1954). Thus, while all members of the herd engaged in approximately the same number of interactions per unit time, the number of encounters tapered off rapidly as rank separation increased (Figure 15). This phenomenon

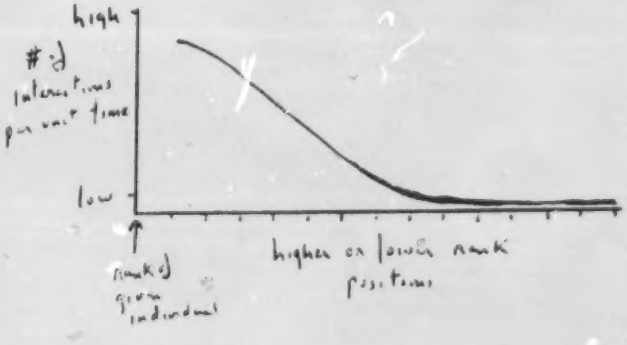


Fig. 15. The relationship between separation in ranks and number of interactions.

suggests that the alpha animal is not busily engaged in suppressing all the others in the group; instead, she has only to deal with a few of the high ranking animals and more or less ignore the rest. It also suggests

that the omega animal does not suffer at the (figuratively speaking) hands of all other members of the group, which probably would be fatal in a large group; instead, she has mainly to cope with a few superiors, most of which are also low ranking.

Hierarchy and Individual Recognition

It is also important to note that the establishment of a hierarchial dominance-subordination social organization implies the ability of individuals to recognize and distinguish among each other and the capability of retaining the information between reinforcement intervals. The problem of retention is not great, since normally group members are in virtually constant contact with each other so that the necessary reinforcements are continuously available. (However, as we have noted previously (page 32) this variable can be artificially manipulated in the laboratory, yielding interesting results.) Similarly, the ability to recognize and distinguish among individuals presents no real problems to a number of moderately sophisticated species. However, the amount of such information that a given individual is capable of assimilating and dealing with is probably very finite, indeed quite limited in a number of species. Just how many other chickens a given bird can comfortably distinguish among and remember on a "first name" basis is unknown. In fact, we do not have such information on any species, including humans. My guess is that few of us would have difficulty writing down one or two hundred names of persons that we presently know or have known in the past (and vice versa), but that beyond a few hundred we would have to do some careful thinking. Certainly it must be a rare person who can come up with a thousand or more friends, relatives and acquaintances; intuitively we would expect that monkeys,

cows, chickens and butterfly fish have significantly lower "upper limits".

The very finite limit to the number of individuals that can be comfortably assimilated may very well be a factor governing the sizes of groups. Let us assume for the moment that the average maximum capacity for chickens is 30 individuals. Therefore, groups consisting of any number of individuals between 2 and 30 could be readily organized into a dominance hierarchy that would serve to minimize the rate and intensity of agonistic interactions within the group. If the group were larger than 30, however, each member would be a "stranger" to at least some others and vice versa; therefore, the average intensity of interactions within the group would rise, and probably the rate as well if density increased with group size. Thus, the larger the group, the greater the level of agonistic interaction, until some new "base level" is achieved; this relationship is shown in Figure 16, which is not surprisingly similar to the relationship shown in Figure 3 (page 29). Indeed, if densities were equated, then Figures 3 and 13 would merge: our chickens in Figure 15 would suffer the high mortality rate exhibited by the rats in Figure 3.

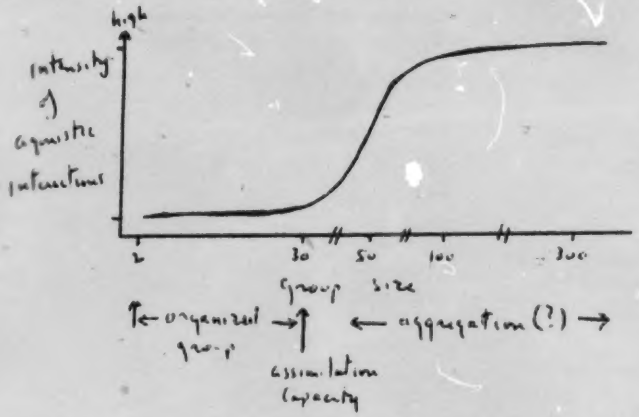


Fig. 16. The intensity of agonistic interactions in relation to group size.

We know that the intensity of agonistic interactions are maintained at a stable minimum in the socially organized group (30 or fewer members). What, then, accounts for the plateau in intensity (disregarding the higher

absolute value) as group size reaches arbitrarily high numbers? (Note that I have established the plateau at some level lower than the absolute maximum possible.) At least two possible explanations come to mind: one is that at high population levels (but remember, not high densities) subgroups would be formed, each consisting of 30 or fewer individuals, and the higher intensity level is a function of interactions between members of different groups. A second possibility is that subgroups are not formed and that the higher population levels are truly aggregates; since density is not increased, the higher intensity level is simply a function of the number of other birds a chicken is likely to encounter and have to compete with in the course of its normal routine daily activities.

At this point the ideas presented above are mostly speculative, but intriguing. There is some evidence for rejecting the notion of subgroups, however reasonable it may have appeared at first. Some years ago, Hale (pers. comm.) casually marked about 10-20 chickens in one small area of a large chicken house that contained some 5000 hens; the expectation was that the marked birds, since they were together at the time of marking, would be reasonably close together during at least the ensuing few days or weeks, and in fact would not stray very far from the area in which they were marked; that area might more or less constitute a "base range" for the subgroup. Unfortunately, the hypotheses had to be completely abandoned: by the next day and thereafter, indeed before the first day was over, the marked birds were randomly distributed throughout the chicken house, both with respect to each other and with respect to location. Replicates of this simple experiment yielded similar results. Rejecting then the notion of subgroups, we are left with the alternative

idea that while dominance hierarchies function smoothly at fairly low population levels, overwhelmingly large groups must operate as unorganized aggregations. But since aggregations provide fewer benefits to the members than do organized societies, it follows that selection would favor the (smaller) social group rather than the (larger) aggregate. Hence, average group sizes (so commonly reported for many species in the wild) may be governed as much by the behavioral "assimilation" capacities of the species as they are by "carrying capacities" of the physical environment.

Of course, rejecting the notion of subgroups in chickens does not mean that we must reject this format in other species as well. Far from it: the literature abounds with descriptions of subgroupings in small organized groups as well as in large aggregates. The juvenile peer playgroup of the Anubis baboon troop exemplifies the former, while the family unit subgroup of the Hamadryas baboon aggregate troop serves as an example of the latter. I suspect that the huge migratory herds of African herbivores is essentially an aggregation of parent-young subgroups.

Hierarchy and Limited Recognition Abilities

Up to this point we have been dealing with species that are characterized by abilities to distinguish among individuals and retain the distinctions for reasonable periods of time. In such species, e.g., chickens, cows, various primates, to name but a few, hierarchies are quite stable over time so long as the resources are adequate and agonistic interactions are therefore minimized. But what is the situation in the social species that have very limited individual discrimination or retention abilities? The answer is that organization might still be possible, but it would tend to be based more on "lumped classes" rather than on specific individuals.

The simplest class dichotomy is "insiders" versus "outsiders"; an individual need only distinguish between those that are members of its own group and those that are not. If the "inside" group is small, say a breeding pair and its brood, then the job can be handled by fairly unsophisticated discrimination abilities; in fact, the job can be made even simpler by the utilization of terrain features to create geographic boundaries. This situation is perhaps best exemplified by the perching song birds, whose territorial arrangements during the breeding season have been discussed earlier.

If the "inside" group is large, as can often be the case, then the problem of dealing with overwhelming quantities of information can be obviated by the establishment of a few manageable and readily identified "classes" within the group. Any clearly identifiable feature can be used to distinguish between classes: size, sex, color, even odor. In the social insects, where huge groups are common (e.g., 40,000-60,000 individuals in a honeybee hive), a chemical label distinguishes between "insiders" and "outsiders". Other chemical labels are used to identify workers (sterile females), drones (males), the single queen (a fertile female) and developing larvae.

Whatever the basis for distinction, individuals respond consistently to all members of a class so that in fact hierarchial organizations along class lines becomes possible. In large mixed-sex flocks of chickens, adult males as a class are dominant over adult females, i.e., the lower order males are dominant over the higher order females. In domestic turkeys, Hale (1957) reported consistency in hierarchial arrangements of mixed-variety flocks: "Blacks" always dominated "Bronzes" who in turn were always dominant over "Narragansetts" and "White Hollands". Crayfish

(Orconectes virilis) normally live in small burrow-territories that they vigorously defend from intruders; thus, individual discrimination is unnecessary (and probably impossible) in the species. However, in a laboratory situation where four crayfish were put together, an hierarchial organization was quickly established. The hierarchy was correlated with size: individuals attacked smaller crayfish and deferred to larger ones, regardless of sex (Bovbjerg, 1953). We may well ask how the individual crayfish "knows" its own size; so far as I know, the question remains unanswered.

Stability of Hierarchy

The stability of an hierarchial order is directly related to the availability of resources. Although the higher ranking animals derive benefits and privileges according to their rank, when resources are plentiful or at least equitably distributed, there is little conflict between the higher and the lower animals; the few benefits that accrue to the higher order animals are apparently not worth much fuss and bother. Schein and Fohrman (1955) found that the rank order in a closed herd (individuals from the outside are rarely, if ever, introduced; recruitment is almost exclusively by way of birth) of dairy cattle was absolutely stable over a period of years; with all their needs met by proper management techniques, the cows had little if any compelling reasons to compete.

When the spread of benefits between higher and lower order animals is great, i.e., when competition for living essentials is severe, then the hierarchy is likely to be quite unstable. We observe much instability in wild rats, with resultant continuous disruption of social bonds as formerly dominant individuals and unsuccessful contestants are forced to emigrate.

Between the extremes represented by cows and rats, we should cite an interesting cyclicity observed in domestic turkeys. In pens containing 20-30 females, the rank order was reasonably stable from week to week and from month to month. There were changes, of course, but rank order positions varied little from one observation period to another. During the non-breeding season, pens of males were much like the females, with rank reversals occurring between observation periods, but few major shifts in positions. However, during breeding seasons the male rank order was in continual turmoil, with major shifts occurring from week to week. Apparently, sexual partners, even as potentials, become a commodity in short supply.

Territory

The concept of "territory" came to prominence following publication of Howard's book, Territory in Bird Life (1920); Howard defined a territory as "a defended area", and in the main this definition persists to the present. It is not my intention here to elaborate extensively on this important ecological concept nor to provide an exhaustive review of research on territory. Instead, I wish only to examine briefly the relationship between territorialism and some of the concepts with which we have been dealing, such as hierarchy.

We have already pointed out that species that are characterized by the establishment of territories may also show limited inter-individual recognition capacities and concomitant increased stereotypic behaviors. Stimuli releasing social behaviors tend to be fairly simple (e.g., the red coloration on a male robin's breast, the shoulder epaulette of male

red-winged blackbirds; the swollen belly of a ripe female stickleback fish) and the animals are easily fooled by models and mimics. Still, the individual is alpha animal in its territory, or it shares a high ranking position with a very few selected others. The territory owner can operate on a simple insider-outsider system, or, as is probably more commonly the case, can also recognize and distinguish among its neighbors in adjoining territories. In any event, the total number of distinctions that the individual must make are few and require minimal cognitive abilities. Social structure of the breeding colony as a whole is of the aggregate type: each "unit" consists of a breeding group with its inherent organization, but all units are equal and all are performing the same roles as far as the colony as a whole is concerned.

In an effort to discover if there was any firm relationship between hierarchial and territorial social structures, we (Salomon and Schein, unpulb. ms.) released an established group of 12 roosters into a 10-acre pasture that contained a surplus of roosting pens (each pen capable of housing 40 or 50 birds) with food, and water available ad lib. in each

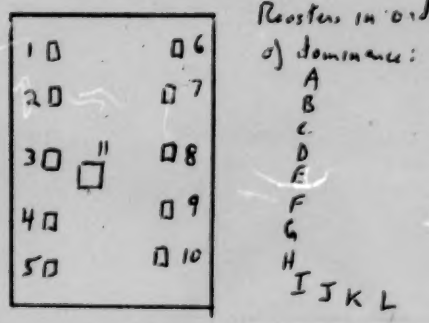


Fig. 17. Arrangement of pens (food, water, roosts) in a 10 acre field.

pen. Some 30-40 hens were also introduced, and the now mixed-sex flock established itself in and around roosts 3, 4 and 11 (see Figure 14), with most of the birds confining themselves to the immediate vicinity of roost 3. The omega rooster, L, quickly left the group and wandered extensively over the field; he slept alone and in a different roost each night and was

dead by the third day. The new omega rooster, K, also left the group, wandered for a few days, and died soon thereafter.

About the same time, rooster D split away from the group and established himself in and around roost 8 with a few females. He was soon joined by male F, and between the two of them they extended their now firmly defended territory to include roost 9 and most of roost 11. Another male, H, moved to roosts 5 and 10 with one female, but his defensive strategy was simply to avoid the other males if they invaded his area (and at the same time trying to keep his female from being "captured" by the invaders). Males D and F, on the other hand vigorously and successfully defended their jointly owned territory from intrusions by males of the original main group, including males A, B, and C to whom they had previously deferred. Indeed, a fair amount of time was spent in "border patrols", with D and F on the one side and one or two members of the original group (including lower ranking males) on the other. The border patrols seemed to serve three purposes: (1) keep the "outsider" males out; (2) keep the "insider" females in; (3) try to "capture" outsider females.

Throughout all these observations, the females seemed quite unconcerned with the machinations of the males. We have no observations of the female social structures, but they seemed to spend most of their time feeding, preening, tidbitting, and otherwise tending to their own business. They did not seem to have vested interests in any one territory or any particular grouping of males; our impressions were that they would have freely moved from one group to another had the males permitted them to do so.

That the "territory" was more harem oriented than geographically based was evidenced by the number of occasions that the D-F females wandered

down to the vicinity of roost 10 for a few days; D and F would move with them, thereby abandoning the border around roost 11, and of course H would herd his female to roost 5. Some of the main group males (and females) might wander over to the temporarily abandoned roost 8, but they never firmly established themselves there and always returned to the main group in roost 3. After a day or two, the D-F group returned to its original base at roosts 8-9, H and his female wandered freely between roosts 5 and 10, and border patrols around roost 11 were re-established. The main group also "wandered" to roost 4 on a couple of occasions, temporarily abandoning roost 3, but always returned to the old positions within a few days. Within the main group, the remnants of the old male hierarchy persisted, with perhaps one or two minor adjustments. The relationships among the surviving 10 males is shown in Figure 18.

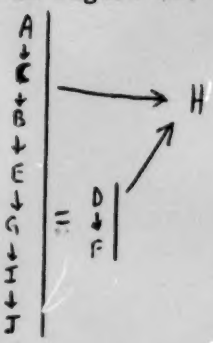


Fig. 18. Relationships among the surviving 10 males in the "Territory" experiment.

After a few weeks, the hierarchial-territorial blend was disrupted by gradually reducing the space available to the birds, until eventually the males were back to the original 12' x 12' size pen from whence they started. Interestingly, as the space disappeared and the territories were disrupted, the males that had left the main group now moved back into the main body and assumed essentially the same ranks they had at the outset; the final rank positions are shown in Figure 19.

Fig. 19. Relationships among the surviving 10 males after the "Territory" experiment.

A → C → B → D → E → F → G → H → I → J

A replication of this study yielded very similar results: the lowest order males wandered away from the group and died shortly thereafter; the middle order males moved out with a few females and established territories apart from the main group. When the birds were reconfined to the original small area, the males resumed essentially the same rank positions as they held at the outset.

Some interesting conclusions might be drawn from this study. One is that a hierarchially organized group retains essentially the same basic structure even if space and resource constraints are removed. A second is that a hierarchially organized group will rapidly establish a group territory once it is confronted with the threat of a neighboring group. A third, and perhaps more tentative conclusion, is that the pressures of an organized hierarchy are most severe on middle and lowest ranking animals; they are the ones to leave when space and resource constraints are lifted. The lowest ranking animals are probably forced out while the middle ranking animals are most likely to strike out on their own.

Home Range

The home range of an animal encompasses the geographical area in which the animal moves about in the course of its daily existence. It is often somewhat nebulously defined in that ranges may shift from time to time, say from season to season. However, given a fixed time interval, the home range of motile forms can be reasonably well specified in most cases. Exceptions might be those animals that drift about as a consequence of physical forces, such as winds or currents; they are likely to not be confined to a definite area except in the broadest geographical

sense. Another exception might be those animals that wander continuously and extensively, rarely covering the same ground twice in a year; such a beast is the Polar bear (Thalarctos maritimus), who for the most part inhabits an environment with few if any fixed features useful for orientation.

Despite these exceptions, most animals confine their daily activities to a fairly definite piece of geography that contains the necessary requisites (food, water, shelter sites, etc.) for survival. Home ranges may be stable throughout most of the life of the animal (such as rats at a city dump), or may be seasonal in nature (such as in the migratory forms, which essentially have at least two disconinuous home ranges), or may change according to other temporal factors. Several years ago, a group of us in Baltimore plotted our "home ranges" over a two-week period using methods then in vogue for determining home ranges of mice: we "trapped and released" ourselves every four hours, i.e., we recorded our locations at four-hour intervals and then plotted the locations on a master map of the city and county. We gained only a little more information when we doubled trapping intensity (i.e., marked locations every two hours) or when we trapped at random times throughout the day. It was surprising to each of us to discover how limited were our "home ranges": for most of us there was a cluster of capture points around the home (the "nest") and another cluster of points around the school (the "foraging area"), with little in between. Most "nest" trappings occurred in the evenings and most "forage area" trappings were made during the daytime hours. One "mouse" differed slightly from the others: it had a third cluster of capture points in downtown Baltimore and some random points throughout the city; as it turned out, that mouse drove a taxicab part-

time during evenings and weekends. All home ranges overlapped almost completely in the forage areas but there was little if any overlap at the nests.

The data were remarkably similar to data obtained with wild rats (Rattus norvegicus) in a city dump, with house mice (Mus musculus) in an abandoned house, and with deer mice (Peromyscus spp.) in the field. The nest site and its immediate environs might be considered an exclusive (probably defended) territory, while the forage areas are more or less shared by all. Occasional stray captures might represent exploratory wanderings that could eventually lead to extension of home ranges or shifts to new areas.

Group Ranges and Organizations

Just as individuals in loosely organized colonies (e.g., rats, mice) have reasonably well defined home ranges, so do well organized groups (e.g., primate troops, wolf packs). Here, the home ranges of each member of the group overlap completely, and if the range is defended, then a group territory exists. More often than not, it is impossible to defend an entire extensive range, so the range is a territory only in sense that there is no temporal overlap between "owners" and "intruders"; if overlap does occur, then "intruders" are repulsed by "owners".

The organizational structure in Anubis baboons (Papio anubis) has been extensively studied by DeVore and his colleagues, (e.g., DeVore and Washburn, 1961)
/and might serve as a typical example of group structure (if any one example may be considered "typical"). Troops average about 40 individuals, and each troop has a rather extensive home range which overlaps

with the ranges of neighboring troops. Meetings with neighboring troops are usually peaceful occasions with free intermingling lasting for a few hours to a few days. The organizational structure within the troop is sharply defined and consists of a few classes of individuals, each with a different role to play. The classes are often spatially arranged in roughly concentric circles, with the dominant males in the center (the central hierarchy); succeeding circles include females with infants, females with older young, females without young and younger juveniles, older juveniles, young adult males, and finally older adult (peripheral) males. According to DeVore, the central hierarchy males act as "leaders": they determine the direction and extent of troop movement; they maintain order in the troop by intervening in the event of serious squabbles among females or among the juveniles; they play a prominent role in defense against predators; finally, while paternity in a baboon troop is difficult to ascertain, they probably sire a disproportionately high share of the young since they seem to mate when the females reach the peak of receptivity.

The role of the adult females seems to center about the production, care and protection of the young. Juveniles have no responsibilities other than to take care of themselves and to grow up; older juveniles, expecially males, might on occasion join in anti-predator defenses, but otherwise their role is fairly simple. As older juveniles mature, the newly adult females join the adult female pool while the newly adult males move to the group of peripheral males. When a predator approaches the troop, it is most likely to encounter a peripheral male who must therefore be wary. If the peripheral male fails to spot the predator, then its death thrashings will serve to alert the group and permit them to

escape. If it does detect the predator in time, then its alarm call will bring forth the central hierarchy males as well as other peripheral males, while the females, infants and juveniles will escape to the trees.

Mortality among peripheral males is obviously high when compared to mortality rates in other classes. However, the survivors serve as a pool of potential replacements in the event a central hierarchy male dies or is otherwise deposed. A deposed central hierarchy male is usually well past his prime and approaching old age. As he falls from the hierarchy, he moves out of the center and becomes a member of the peripheral male class. With increasing age comes increasing debility and hence even "further out" peripherialism, where he is especially prone to predators; solitary baboons do not last long.

Leadership

If we operationally define a "leader" as an individual that consistently directs the movement of a group through space, then the phenomenon of leadership is common throughout the animal kingdom. Further, leaders are often at the forefront of a movement and are frequently responsible for initiating a movement or an activity. I wish here o examine the concept of leadership and will propose that in many cases, the active priniciple may be <u>followership</u> rather than <u>leadership</u>.

First, though, let us separate "dominance" from "leadership". While in elephant and Red deer herds the dominant female consistently is at the forefront in a move (and hence a leader in the sense that she is determining the direction that the group will take), and in Anubis baboons the central hierarchy males determine the direction of movement even if they are not at the forefront, the dominant animals need not necessarily

serve as leaders. In cows, sheep, and goats, leadership (if any) roles are often assumed by non-dominant animals. Chicken and turkey flocks are usually "leaderless" in the sense that no one individual is consistently at the forefront; "forefronting" is a happenstance and random occurrence among the females. The males, despite clearcut dominance stay with the females and only occasionally exert directionality influences in that they keep the females away from outside males. Other than being "protected" from outside males, it is the females that determine the direction of movement of the group and that initiate most activities.

There are many examples of "leaderless" groups among the social species, in that movements are not consistently directed by any one individual. However, no case comes to mind that does not provide examples of acute and active following. The forager honeybee that stumbles acorss a choice food source and passes the information on to her hivemates (see Exercise 2) is temporarily a leader in that it is initiating a particular movement. However, as recruitment of more and more foragers progresses, each new recruit is at first a follower and then perhaps a leader of even newer recruits; leadership and followership is thereby distributed among all the bees attending to the food source. In the migratory movements of Army ants (Eciton spp.) no one individual seems to be setting the course to be followed; instead, the push is from the rear and the forefront tumbles over itself in sort of a rolling wave movement. An individual may scurry out a bit, followed by another that scurries a bit further and so on; the entire group moves. Other examples of "leaderless" groups may be drawn from herding and flocking animals where the group consists of many rather than one or a few family lines; elephants in large composite mixed-sex many-family herds are probably also "leader-

less" as a group. Schools of fish are leaderless; individuals coordinate movements with each other in a tightly organized spatial arrangement. As nearly as can be determined, any individual may direct the movement of the school at any given moment (Shaw, 1970). The key point is that no matter which individual momentarily leads, all the others avidly follow.

We are now in a position to look at the phenomenon of leadership more closely. In the herd of dairy cows that we studied (Schein and Fohrman, 1955), one cow was decidedly a "leader"; she frequently was at the forefront of herd movements and often could be identified as the initiator of group activities, such as going to water or starting to graze after a period of lying down. This cow had been brought into the herd shortly before reaching maturity; most of the other herd members had been born into the herd. At the time these observations were made she was a high ranking and senior member of the herd, but was clearly not the most dominant; in fact, she was outranked by several younger, as well as older, cows. One notable trait that set her apart from the others was just that: she often stood somewhat apart from the group. Observations of this cow and several other "leader" cows and sheep led me to hypothesize that "leadership" is simply a matter of the lead animal being able to tolerate greater separation distances from its neighbors than they can tolerate from it. It is not that the leader is actively inducing the others to follow but rather that the followers are unwilling to be separated from the leader.

A postulated model for leadership can be built around the concept of Inter-Animal Distance (IAD; cf. pages 24-28). Suppose a small leaderless group of animals were resting in a field, and that the average IAD tolerance range was between 3 and 10 units; individuals closer than 3 units

from each other would move apart, and no individual would be more than 10 units from its nearest neighbor. A possible arrangement of the resting group is shown in Figure 20).

Fig. 20. Possible spatial arrangement of a group of resting cows.

Should any one stray more than 10 units from its nearest neighbor, then it would return unless the neighbor moved to compensate for the now unacceptable IAD. For example, if individual A in Figure 20 moved beyond the 10-unit limit, none of its nearby neighbors (D, B, F) are likely to be affected because each is well within 10 units of another (D near B and C; B near D, C, and E; F near E and J); therefore, A is likely to return to the proximity of at least one of the others. However, if L happened to wander out beyond the 10-unit limit from K, K might move to adjust since it is just about at the maximum allowable distance from J. If K does move out with L, then J is forced to a decision: it is nearly at maximum allowable distance from F and I. If it elects to move with L and K, then sufficient momentum might be generated to move the entire group, and L will have emerged as a momentary "leader". Of course, if the group does not follow, then chances are that the subgroup J, K, and L will quickly rejoin the main group again.

If, for one reason or another one of the members of the group differed from the average in its maximum allowable IAD (say, for example, its

IAD range was 3-15 units while the others remained at 3-10), then that individual would likely emerge as a "leader" simply because it could comfortably move further away from its nearest neighbor than the neighbor could comfortably tolerate. Should the neighbor not move because of the proximity of other neighbors, then the leadership would be aborted and the potential "leader" would rejoin the group (but could still comfortably remain a somewhat greater distance away from the others). In essence, then, the "leader" is an individual that is less well integrated into the group than the others. Of course, some sort of balance must be struck between lesser integration and outright non-members; an individual that is so poorly integrated as to be almost an outcast is not likely to attract many or any followers.

IV. COMMUNICATION

Communication means many things to many people. Even among people with common interests, wherein a jargon indigenous to a technical field usually develops, a commonly accepted exclusive interpretation of the term is lacking. Behaviorists use the word communication in two related but somewhat different contexts: the first, which is sometimes called "passive communication", deals with information gathered by an individual via any perceptual channel. The stress is on the gaining of information and information theory. "Active communication", on the other hand, is more restrictive and deals with the transmission of information from one individual to another. The emphasis is on the transfer of information in addition to its perception or gain. Our treatment here is concerned with what I have termed "active communication", which is so important in and fundamental to biosociological systems.

In the simplest communication system, there must be a sender, a receiver, and some sort of channel or physical link between the two. The channel is open in both directions so that feedback is possible. The interpretation and subsequent study of communication signals is based on the premise that signals used in communication are relatively specific and unambiguous, i.e., the signal to noise (S/N) ratio is high. The techniques of studying communication systems are essentially the same, no matter which channel of transmission is involved. The observer in the field tentatively interprets a signal on the basis of the behaviors of the sender and the assumed receiver before, during and after the signal. The signal is then reproduced by the observer and transmitted to receivers under controlled laboratory conditions, thus confirming or negating tentative field interpretations.

Most animals have several systems for gaining information from the environment and from other individuals. Chief among these involve specialized organs for visual, auditory, tactile, and chemical perception which thereby define the physical channels that can be used for communication between individuals. In order to take account of perceptual mechanisms of the receiver, the sender must translate information into a recognizable form. For example, in birds an emotional state must be transformed into a visual, auditory or tactile signal, since most birds have only limited chemical perceptual abilities.

Passive and Active Communication

The distinction between "passive" and "active" communication is often subtle and complicated further by the phenomenon of delayed responses to communication signals (see Primer Effects, below). Passive communication, in the way I am using it, deals simply with the gathering of information no matter what the source. While walking along a forest trail or a city street, we step around perceived obstacles such as trees or walls; our perceptual mechanisms tell us that there is a tree or wall in the direct path, and we have long since learned that trees or walls are easier to walk around than through. Neither the tree nor the wall is "communicating" with us in any sense; they are not what I would consider active "senders", even though we in fact are active "receivers" of the information. The circuit is not complete: we are the receivers, the perceptual channel is defined (visual and tactile), information is gained, but there are no senders nor is there any feedback in the system; we are not reinforcing "treeness" or "wallness" by avoiding the obstacles.

There is, however, a significant difference between the tree and the wall. While the wall itself is not communicating with us, the person who built the wall may in fact have done so for purposes of communication. The signal is usually clear: "Keep Out"; and as soon as we receive the message the circuit with the other person is completed and communication, with feedback (our avoidance) is effected. But suppose that for one reason or another we chose to ignore the "Keep Out" message; we climbed over the wall and continued on our way. The feedback would dictate to the wall builder that the signal is not an effective deterrent, that additional measures are necessary if the message is to be responded to in the intended manner. On the other hand, the wall builder may no longer be concerned about our transgressions, having left the area years ago; in this case, feedback is not effected.

The episode with the wall and the tree illustrates a number of points and perhaps helps to operationally define several of the concepts with which we are dealing; they are worth repeating:

1. Our perception of the tree and the wall is a matter of simple information gathering.
2. Our responses to the newly gathered information are governed by our past experiences with these or similar objects.
3. In the absence of a "sender" and feedback, communication is at best passive; such is the case with the tree (assuming, of course, that it was not deliberately planted by somebody to impart information to others).
4. In the case of the wall, its builder is actually a "sender" and so an active communication circuit could be completed.
5. If feedback is effected, then active communication is completed.

Just as the "sender" is necessary in active communication, so is the receiver and the completion of the feedback loop. The person who built the wall is putting out a continuous signal, but until we perceived and responded to the wall, communication was not achieved. We (Schein and Hale, 1965) have applied the term "broadcast" to these situations where a sender and a signal, but no receiver, exist at the moment. All that is needed to effectuate communication is the receiver. This situation is far from uncommon in the animal world: early courtship or "advertising" calls of many birds, scent markings of various mammal species, and coloration patterns of various fish serve as examples.

Let us now examine a mating sequence of turkeys from the point of view of communication.

At the outset (Step 1), the male performs a courtship strut, an elaborate combination of stereotyped postures, movements and sounds. This is in effect a broadcast signal much like the vocalized "gobble" calls that he may have emitted earlier. Presumably the gobble calls served to advertise his presence to others, male and female alike. The difference between the strut and the gobble broadcast

signals is that the gobble, being almost entirely an auditory signal, can carry quite some distance while the strut, which is mostly visual, depends upon line-of-sight for reception. Either signal may be completely ignored by others of either sex or any age: communication is not necessarily effected, at least so far as we can detect and measure.

If, however, in response to the strut, another bird crouches (Step 2), the strutting male will respond by approaching; the croucher will in turn elevate its head somewhat, and the male will proceed to mount (Step 5). We (Schein and Hale, 1965) have labeled these preliminaries as "identifying" signals: active communication was effected as soon as the female responded (Step 2) to the male's broadcast, and what followed were a series of communications whereby each determined the appropriateness and willingness of its partner. Had the male not approached the crouching female, then she would have eventually gotten up; the strutter was not a potential mating partner. Similarly, if the croucher would have gotten up and moved away upon the approach of the male, then he would have reverted to broadcast strutting; the croucher was not a receptive female. Of course, communication signals being as imperfect as they are, the jilted partner in either case would probably make a few more attempts before moving away completely: the female would recrouch nearer to the strutter, or the male would continue to strut while following the once-crouched individual.

By Step 6 (Figure 21), identification of each partner is more or less complete; it is unlikely that things would have progressed this far if one of the two birds was not in fact a sexually active male and the other a sexually receptive female. There remains, then, a series of small steps designed to synchronize and mesh the different motor actions of each

partner. Each step is in response to signals (predominantly tactile) each receives from the other, until finally the mating act is completed. The synchronizing signals involved in Steps 6-12 are obviously essential to the successful completion of the act, and represent perhaps a prime example of active communication.

Signal Effects: Releasers and Primers

We have indicated above that a common study technique in communication research is to present the signal under controlled laboratory conditions and observe the response of the receiver. The drawback to this approach is that responses are not always so amenable to the observational techniques used to measure behavior or worse yet, they are not always immediate. Recording nerve impulses from the auditory nerve of a cat tells us that the cat's brain is indeed receiving representations of the click sounds that we are generating, but unless the cat does something as a consequence of the clicks we cannot really say that communication has been effected. As I write these golden words, I am generating a series of broadcast signals which you may or may not choose to read. Should you not read, all well and good: communication is not accomplished and that is clear. But if you do read, then I still do not know if communication has been achieved until there is some response on your part. If you respond with "My, what a pretty color" or "How nice", then I wonder if there has been communication. If you leap up and shout "What rot!", then at least I am getting a response which suggests that you have in fact been reading. If you attack my arguments in a meaningful fashion, then I have more confidence that communication has in fact been achieved.

Suppose you do read but say and do absolutely nothing in response.

Has my signal been received? I cannot know, and in the absence of a response would probably assume that it has not been. Yet, some time later you may do something that in some tortuous way can be traced back to your actually having read. Communication was indeed achieved, but the response was delayed and was proferred in an unanticipated manner. This characterizes the problems facing those communication researchers who are dealing with "primer" rather than "releaser" effects: there is clearly a sender and a signal, but the response of the receiver is delayed for some period of time, thus delaying the feedback signals; by the time the response is forthcoming, the sender may have disappeared or may be in a completely different motivational state.

A good example of the primer effect of a signal is offered by Marshall (1975). He found that adult female Mozambique mouthbreeder fish (Tilapia mossambica) held in social isolation spawn at regular intervals, the period ranging from a low of about 14 days to a high of over 30 days but consistent within females. Thus, following spawning (day 0), the time to the next regular spawning could be predicted with a fair degree of accuracy. However, if on day 0 a female is exposed to only the acoustic signals emitted by a courting male, she spawns some 7 days earlier than she would have had she not been exposed to the signal. Had the primer effects of the acoustic signals not been detected, the communicative value of the males' signals would not have been recognized.

Aside from considerations of possible priming effects, the signals that we more commonly observe and study have an immediate releaser effect:

they elicit an immediate response on the part of the receiver. Signals may affect direction (towards or away from the producer) or rate of movement of the receiver. A ripe female cricket (fam. Gryllidae) approaches a male in response to his broadcast or advertising call. As her presence is detected, his call changes and she stops approaching (identification signals); those that do not stop are thereby distinguished from receptive females. Chicken or turkey mothers emit one type of clucking call that chicks respond to by remaining in the mothers' general vicinity; a different call will send them scurrying away from her, and a third call will bring them to her. Various research workers have identified some 35-45 distinct vocal signals (to say nothing of visual signals) in the repertoire of the domestic chicken. Some signals are species-typical, in that there is little variation among individuals: if you've heard one chick distress call, you've heard them all! Other signals, such as the crow of the rooster, are highly variable and in fact can serve as individual "markers": Siegel and his colleagues (1965) were able to distinguish among 20 roosters on the basis of their crows alone.

Signals also convey information about the sender, such as its physiological state or even just its location. The sparrow that so happily chirps on the tree in early springtime is essentially broadcasting his availability to a potential mate and at the same time warning other males to keep away from his territory. Likewise, fireflies and spring peeper frogs are advertising their location and sexual availability, even if they care little about territorial defense. But in all cases, the boldness of the signal must be tempered by constraints imposed by potential predators, as we shall see below.

Evolution of Communication Systems

All organisms are endowed with systems for detecting changes in their immediate environment: the irritability of tissues is a basic property of living matter. In the course of time, more sophisticated environmental sensors evolved: from very primitive general irritability to more specialized systems for detecting changes in pressure, pH, temperature, light, and so forth. Concomitant with the evolution of detection systems was the evolution of coordinated motility or the ability to respond to environmental changes. In response to an increasing environmental temperature, the more sophisticated animal could now move and thereby increase the probability of finding a more equitable spot. The elaboration of sophisticated environmental sensors meant the elaboration of information gathering and integrating capacities of organisms: the development of nervous systems and brains. With the advent of the most primitive forms of social behavior, such as sexual reproduction, the role of the sender now had to be developed: information had not only to be passively gained, but steps had to be taken to positively influence the acquisition of the information. In other words, ways and means of sending information had to be devised. Thus, mechanisms to create sounds or to elaborate particular chemicals were a logical next step in development.

It is not difficult to offer speculations on the development of a particular signal. Tinbergen (1952) suggested that a generalized posture or movement could be converted into a useful signal by the process of "ritualization"; the exaggeration of the posture or movement which thereby permits the receiver to more readily distinguish the signal from background "noise". The elaborate courtship strut of the turkey, for

example, probably stemmed in small steps from a simple walking approach. Selection would have favored the development of some way of distinguishing between a walking approach that ends in a mating from a more or less random movement. Thus, a stiff-legged gait invoked only in appropriate circumstances would take on signal value because of its discernability from the ordinary gait: the signal to noise ratio is increased. To the extent that the signal makes for more efficient mating, it will be selected for and would thereby be elaborated even further to increase the signal to noise ratio. Hence, the development of some rather fancy courtship patterns in various species.

There are two brakes to the continuous elaboration of a signal. The first occurs simply when further elaboration fails to confer any further advantage to either the sender or the receiver. The signal to noise ratio is maximal, i.e., the signal is so clear and so unambiguous that the probability of not being able to distinguish between it and background noise is very small. In this case, the signal should pretty well stay where it is, or perhaps drift in a somewhat random fashion.

The second brake is probably more common: it results from the pressure of increasing disadvantage. Selection will favor the elaboration of a signal so long as the advantages outweigh the disadvantages. When the disadvantages begin to outweigh the advantages, selection will be against further elaboration. Disadvantages may accrue in a number of ways, but all add up to the increased vulnerability of the sender: a more elaborate signal might be so physiologically expensive that it significantly decreases overall efficiency or might simply be more likely to attract unwanted predators. Hence, some balance must be struck: the signal must be sufficiently clear so as to minimize the probability of misinterpretation

by the intended receiver; it must also be sufficiently vague so as to maximize the probability of misinterpretation by unintended receivers, such as predators. Feedback from the intended receiver will produce pressure to maximize the signal to noise ratio; feedback from unintended receivers will produce pressure to minimize the signal to noise ratio, i.e., to introduce as much noise as possible into the system.

Channels of Communication

Communication channels are defined by the perceptual capacities of the intended receivers. I do not wish here to go into perceptual mechanisms and species-typical capabilities to any great extent, but rather to present a brief overview of the major communication channels used in social interactions. Specifically, we shall examine some of the characteristics of acoustic, visual, tactile and chemical signals. Recognize, however, that an animal generally uses several channels simultaneously, the information received through one channel being supplemented by information received through another.

Acoustic Signals

Sound signals have certain advantages over other channels in some circumstances and of course certain disadvantages in others. One advantage is that they may be transmitted over moderate distances in air (enormous distances in water) and can go around or through many barriers. Thus, clear line-of-sight is not necessary in broadcasting a sound signal, although increasing the number of barriers certainly increases the attenuation of a signal. Sound is multidirectional: properly launched, the signal can be picked up by receivers scattered throughout a full 360°

circle. More commonly, though, the signal can be channelled so as to be stronger in one arc of the circle than in others. A distinct advantage of sound is its independence from light: it is equally effective, day or night. In fact, sound as used in communication is relatively independent of most environmental variables within the ranges affecting living systems: light, temperature, pH, density of the medium, pressure, etc.

Sounds may be modified along three major dimensions (frequency, amplitude and time) to produce an infinite variety of signals. Thus, acoustic communication has great flexibility and is widely used in social interactions, especially among vertebrates. We have mentioned earlier that the acoustic repertoire of domestic chickens includes some 35-45 distinct sounds; no doubt acoustic repertoires of many species (not counting humans) equals or exceeds that of the chicken.

Acoustic communication does have several disadvantages. For one, it is temporally bound: the sound produced exists only as generated and does not persist. The cricket that advertises its presence through sounds must continue to emit chirps; when it stops chirping, its advertisement disappears. Of course, the non-persistance of the sound signal could be advantageous in certain situations, such as when hiding from a predator or when the signal no longer serves a useful purpose. A more serious disadvantage is its rather finite range: sound signals are fine for moderate distances, but useless at long ranges (in an air medium), especially if a few barriers (such as trees) are interposed. Thus, acoustic communication operates most efficiently at moderate and short ranges; within such ranges, the relatively slow speed of transmission (as compared to light) is not only no real problem but in fact is important in localization. Sound travels some five times faster in water and is significantly less

attenuated in water than in air; hence, in a water medium, acoustic communication can involve much greater ranges. It has been suggested that some of the whale sounds recorded in the Caribbean Sea emanated from individuals in the North Pacific!

It would not be particularly useful here to describe endlessly the types and variations of sounds used in communication by various species; but the growing number of species-typical sound catalogues testifies to the widespread use of sound by vertebrates and invertebrates alike. As we have mentioned earlier, sounds in social communication are used to convey location information, to direct movements of conspecifics, and to convey information about physiological condition and/or "emotional" state. Sound signals that are used to convey information on location are segmented or pulsed; the rapid onset of each pulse, such as in a series of clicks, permits the receiver to localize the sound source by comparing the time of arrival at each of at least two separated sound sensors (its "ears"). Chicks under stress (lost or cold) emit loud segmented high frequency sounds known as "distress calls"; the mother answers with a segmented cluck that also facilitates localization, and the two get together.

Signals that are designed to convey other information while at the same time not revealing the location of the sender tend to be continuous, uninterrupted sounds with gradual onsets and gradual, if any, changes in frequency. Threat signals, such as the growl of the dogs are harsh, usually low pitched, often a single relatively long note, and effective at moderate to short ranges. Information about the specific location of the sender is not needed to make the threat effective; all that is needed is to announce presence. Alarm calls are somewhat similar to threats in that localization information is often unnecessary; indeed, revealing the location

of the sender may be highly undesirable. Unlike threats, though, alarm calls are usually loud high frequency broadcast type signals that carry over considerable distances.

An interesting demonstration of the importance of acoustic communication in parent-young interactions in turkeys is provided by Schleidt et al. (1960). They found that normal adult females that were experienced in raising poults (turkey chicks) attacked and killed poults that were "devoiced" (poults that could not make sounds); sham-operated poults were not attacked. The reaction of the hen to the devoiced poults was indistinguishable from her reaction to potential nest predators, such as rats or mice. The hen also attacked and killed all her poults when she herself was deafened; again, sham-operated hens did not kill their young. Apparently, the constant chattering back and forth between the hen and her poults is important not only in the sense of keeping the group together but also in identifying the poults as members of the group. Experience played a decisive role in forming the acoustic identification system: naive young females that had never reared young did not kill the young when they themselves were deafened; they also readily adopted potential predators introduced to the nest. However, if she were not deafened, then she killed those of her poults that were "devoiced" unless all were devoiced. Apparently, in absence of acoustic experience the hen can learn to operate on visual cues, but once acoustic experience is gained it takes precedence over visual information.

Visual Signals

Visual signals, like acoustic signals, are especially useful in some circumstances and utterly useless in others. Although visual channels

are independent of temperature, pressure and pH, they are obviously inoperative in complete darkness and are markedly affected by the density of the medium: unless impeded by barriers, visual signals can be used over enormous distances in air but only over relatively short distances in water. A further complication is that light is readily absorbed or reflected by barriers, so that visual signals are useful only on a line-of-sight basis. Like acoustic signals, visual signals are a "here-now" phenomenon: the signal ceases to exist the moment it stops being emitted. Because of "here-nowness" and the unequivocal directionality imposed by "line-of-sightness", visual signals are particularly useful in conveying precise location information. This may be advantageous or disadvantageous to the sender, depending upon who receives the information. Visual signals in the form of color, movements and postures are also useful, expecially at short and moderate ranges, in conveying information about physiological state: courtship postures, threat displays, and the like. Movements and postures account for a fair amount of non-verbal communication among humans. A signal may be enhanced or obfuscated (i.e., the S/N ratio varied) simply by altering the contrast with background or adjacent parts.

Tactile Signals

Generally, tactile signals can only be used at extremely short ranges, in fact so short that the individuals are in direct contact. Thus, localization information is absolutely precise and immediate. Tactile signals are independent of environmental conditions, such as light or temperature, and are undetectable by any except the sender and the receiver. Thus, such signals are especially useful when secrecy is desirable or imperative; they play a prominant role in synchronizing the mating behavior patterns of each sex. An example of such use is illustrated in Steps 8-14, Figure 21 (see page 121). The use of tactile signals in

conveying much other information is severly limited by the need for immediate proximity of the sender and receiver, and contact proximity in social interactions is restricted to only a few components of the various social behaviors.

Mention should be made of tactile communication that does not involve bodily contact: that of activating pressure receptors through a dense medium, such as water or a strand of a spider's web. Detection of pressure changes caused by movement in water is known to be possible among many fish, especially over short ranges, but the extent to which the channel is used in social communication is not fully understood. Similarly, the extent to which electric pulses emitted by some fish species are used in social communication is relatively unknown. However, that fish gain useful information through pressure and electrical sensors is clear: such information leads to capture of prey or avoidance of predators. More specific information is available in some spiders, where courtship identification signals consist of particular vibrational patterns imposed on the web. The male thus signals that it is a potential mating partner and not a captured prey; interpretation of the signal depends upon the physiological state of the female. In this case, intimate proximity could be fatal if the female happened to be sexually unreceptive at the moment.

Chemical Signals: Pheremones

Just as with other perceptual capabilities, organisms extract much information about the environment by means of special sensors that can detect and differentiate between various chemical compounds in the surrounding area. Those chemical compounds secreted by an individual and used in communication between conspecifics are known as pheremones. This

label was applied because pheremones were originally conceived of as analagous to hormones, the difference being that hormones act within an organism while pheremones act between organisms; pheremones elicit a specific behavior or influence a developmental process in another of the same species. Much of our knowledge and understanding of pheremones is relatively recent: we can demonstrate the presence and action of pheremones, but the chemistry is relatively unknown and the perceptual mechanisms, especially in vertebrates, are poorly understood. Indeed, a fair amount of our information on pheremones stems from work with invertebrates, where chemical communication is especially prominent and significant.

Among the social insects, especially the ants and termites, different pheremones act as trail markers, aggregating substances, alerting substances, aphrodisiacs, and the like. In the social and non-social invertebrates alike, a number of species-specific pheremones have been identified as aphrodisiacs and sex attractants: "seducin" is a chemical compound produced by male Nauphoeta cinerea roaches that attracts receptive females and also serves as an arrestant. Sex attractants in roaches are relatively easy to demonstrate: one has only to establish monosexual cultures (with lots of hiding places) in a jar or terrarium. At some convenient time, a piece of paper towelling that was in the female culture for a day or so is moved to an open place in the male culture. Within seconds, the males swarm out of their hiding places and cover the paper towel with frantic copulatory movements.

Among the fish, chemical perception is highly developed in a number of species and has been implicated in migration, homing and feeding activities as well as in various more intimate social behaviors such as

schooling and reproduction. For example, Bardach /and Todd (1970) found that bullhead catfish (Ictalupus natalis) establish a social hierarchy when they are confined in a tank; agonistic interactions become ritualized and physical damage is thereby minimized. However, if the sense of smell of the fish is destroyed, they cannot form stable groups and therefore fight to the death. Apparently, the fish use chemical cues to identify each other just as the chickens (page 32) used visual cues.

In addition to the individual identifying odors of the catfish (and probably many other species), there is evidence for species-typical odors carried by each member of a species. These odors probably are a component of the mucous slime secreted by the skin and covering the fish, and may be important in establishing and maintaining schools. Various "warning" substances have been identified in fish; these substances are released from the skin of wounded individuals and act much like alarm signals of terrestrial forms in that they bring about avoidance behaviors by others.

What with most birds being anosmic, there is little if any evidence of chemical communication among birds. However, among mammals, the diversity and frequency of occurrence of skin glands and chemical receptors strongly suggest more widespread use of chemical communication in social interactions than was formally supposed. It has long been known that various mammals use urine, feces, and the exudates of specialized secretary glands to mark territorial boundaries, to advertise presence, and to convey information on physiological state. The male dog that lifts his leg and sprinkles some urine on the fire hydrant is essentially laying claim to the area around the hydrant and so informing other interested parties. The female that squats to urinate is simply voiding unless

she happens to be coming into heat; then, she will dribble urine in a number of spots, thereby informing nearby males of her availability.

In cattle on range, experienced bulls often serve as indicators of which females are coming into heat: the males seem to act on chemical cues as they single out and stay near such females fully a day or more prior to overt behavioral manifestations of estrus. The role of experience in forming an association between chemical cues and mating has been demonstrated many times in Artificial Insemination Centers. A bull whose only sexual experiences have been in the collection room where non-estrous teasers are used is not responsive to chemical cues: his performance level is unaffected by the presence or absence of urine from an estrous cow smeared on the teaser.

The study of pheremones among mammals has been made more difficult by the primer, rather than releaser, effect of many of the chemical signals. For example, it is well known that menstrual cycles of human females living in fairly close proximity (such as in a college dormitory or sharing an apartment) tend to become more and more synchronized as the association persists. In mice,

estrus can be induced in segregated female mice by exposing them to the urine of a male; it is a primer effect, in that the estrus follows the exposure by several days. Pregnancy can also be blocked by exposing a female to the urine of a strange male shortly after she has been mated. The specificity of the pregnancy block pheremone is remarkable, in that it is effective only with the same strain of laboratory mouse and has little transferance to other strains.

Chemical signals are highly specific; as Johnston et al. (1970) point out, an equivalent acoustic signal would be a call stimulating only

one type of receptor and heard by only sex and only one age class of a given species. A unique advantage of chemical signals is their ability to transcend the time barrier imposed on the "here-now" acoustic, visual, and tactile signals. The chemical signal released now can still be operating tomorrow or the day after. In fact, the duration of persistance can be modulated to some extent by controlling the volatility of the substance released. Highly volatile substances, such as are used to mark trails in ants, are dissipated moderately rapidly and must be replenished routinely if the trail is to be distinguishable. But that is fine, since it would be quite inefficient to have a trail persist after it is no longer useful. Somewhat less volatile chemical compounds also have their place, such as the queen substance in honeybee hives: so long as the pheremone, produced by the queen, is available throughout the hive, all is well and good. However, if the queen dies or is removed, a notable change in the behavior of the workers occurs within a day or so; the change is attributed to the moderately rapid disappearance of queen substance from the hive. Substances of very low volatility persist for some time and are especially useful as territorial markers; it would do little good if these markers disappeared long before the marking animal had a chance to revisit and remark the site.

Another almost unique characteristic of chemical signals is the limited amount of localization information contained therein. Since the time barrier has been overcome, the receiver can detect where the odor is coming from and may even find the exact spot where the signal has been deposited, but the sender may have long since left the area. This is especially useful if the receiver is a predator, but less useful if the receiver is a desired conspecific (such as a receptive sexual partner).

In such situations, localization can be built into the signal by the simple expedient of not separating the sender from the signal and accepting the risk of attracting an unwanted receiver.

A major disadvantage of chemical communication systems is their heavy dependence upon highly variable environmental conditions. Air and water borne signals are subject to the vagaries of winds and currents; hence, their usefulness for transmission over large distances or specific directions is severely limited (unless such conditions are essentially stable, such as a downstream current). In addition, signals can be masked or obliterated by other environmental variables, such as rain or snow, and volatility is often markedly affected by variations in temperature. All in all, chemical communication is most effective at short ranges in moderately controlled environments such as nests and hives. In the outside world, other systems tend to be more efficient.

Animal Communication and Human Language

Up to this point, our discussion of communication has dealt primarily with what is ordinarily termed "non-verbal" communication. Sounds, movements, postures, smells and pressures are used to convey information on location, to reveal physiological state, to attract or repel, to direct movements, to reveal identity, or to offer some combination of information and directives. In no sense are these various signals akin to words and sentences in human language: the 35-45 sounds in the chicken's vocal repertoire are not words that can be arranged in various ways to convey different messages. If anything, by a wild stretch of the imagination, they might be considered at best /as tangible nouns or simple phrases pertaining

to the immediate situation in which the chicken finds itself, but such an analogy leads to a dead end. It is enough to say that there is a great deal of communication among non-human species, but it is of the non-verbal, non-language type. Without such communication, social interactions and sociality would be impossible. The more highly structured the social organization, the more extensive the communicative repertoire.

Is language then solely a human prerogative? Until fairly recently, the answer was clearly "yes". Now, however, there appear to be significant breakthroughs on the animal language front. After years of trying to teach chimpanzees (Pan troglodytes) to verbalize recognizable words, researchers have hit upon the idea of capitalizing instead on the animal's physical dexterity. In one area of study (Premack, 1971), chimpanzees learn to use tangible objects (such as wooden blocks of various sizes, shapes and colors), each of which represents a discrete object or an operation, to construct sentences and formulate requests. Another ingenious approach has been to teach the rudiments of American Sign Language (Ameslan) to chimpanzees (Gardner and Gardner, 1969, 1971, 1974, 1974). Persons who are well versed in Ameslan (commonly used among the deaf in this country) have little difficulty "conversing" with trained chimpanzees, whose repertoires often exceed 100 words. Washoe, the first chimpanzee to be taught Ameslan by the Gardners, added to her vocabulary by making up signs for some objects and could construct sentences using a simple but logical grammar. She could understand the difference between "you give me" and "me give you", and even generate the chimpanzee equivalent of swearing when the occasion warrants. Since this work is so new and is still in a stage of rapid development, there is little point in expanding on it here since anything committed to paper today will be obsolete tomorrow.

Suffice it to say that the once absolute distinction between humans and non-humans, language, has now been broached; it is no longer so absolute, and with the breakthrough we may learn much about human and non-human societies alike.

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VI. INSTRUCTIONAL MATERIALS

Following is a listing of readings and films that I find especially useful in introducing students to Biosociology. Recognize that this is a very personal list and thoroughly reflects my biases in biology and behavior. Other materials might be more appropriate for readers with different biases, and the reader is encouraged to gather together his/her own list.

A. General References

1. For the more advanced students with at least some background in biology or psychology.

Brown, J. L. 1975. The Evolution of Behavior. New York: Norton, 761 pp. A new book with heavy emphasis on evolution and especially in birds.

Dewsbury, D. A. and Rethlingshafer, D. A. (eds.), 1973. Comparative Psychology. A Modern Survey. New York: McGraw-Hill, 625 pp. The latest updating of an old standard Comparative Psychology text; the various chapters are written by different people, many of which are leaders in their fields.

Hinde, R. A. 1970. Animal Behaviour. 2nd Ed. New York: McGraw-Hill, 876 pp. Complete and very heavy going, but all sides of all arguments are carefully presented and documented; a "must" reference book for serious students of social behavior.

Marler, P. R. and Hamilton, W. J. III. 1966. Mechanisms of Animal Behavior. New York: Wiley, 771 pp. Heavily

slanted towards physiological processes and mechanisms; this book, together with the Hinde book, pretty well cover the field of behavior up to the mid-sixties. It now needs updating.

Wilson, E. O. 1975. Sociobiology. Cambridge, Mass.: Belknap Press. A new book dealing specifically with biosociology, but with a refreshingly new approach; emphasis is on population biology and evolution, rather than simply behavior. The book will be the major one in this field for years to come.

2. For beginning students with little background in biology or psychology.

Eibl-Eibesteldt, I. 1970. Ethology. The Biology of Behavior. New York: Holt, Rinehart and Winston, 530 pp. Provides a good example of the approach prevalent in the European schools; emphasis is on evolution and field biology, with an introduction to human ethology.

Klopfer, P. H. and Hailman, J. P. An Introduction to Animal Behavior. Englewood Cliffs, N. J.: Prentice-Hall, 277 pp. Offers a concise and interesting history of ethology as a field of study; emphasis is on social behaviors and behavioral development.

Manning, A. 1972. An Introduction to Animal Behavior. Reading, Mass.: Addison-Wesley, 294 pp. An easily readable and fairly complete overview of the field of behavior, combining the best elements of different approaches. I have used this one as a "text" in my introductory course.

McGaugh, J. L., Weinberger, N. M. and Whalen, R. E., (eds.), 1967. Psychobiology. The Biological Bases of Behavior. San Francisco: Freeman. A collection of readings from Scientific American. Needs updating.

Scott, J. P. 1958. Animal Behavior. Chicago: University of Chicago Press, 281 pp. An old standby, one of the firsts of behavioral texts that stressed social behaviors; fairly elementary and very easy to read. Useful even at the secondary school level.

Tavolga, W. N. 1969. Principles of Animal Behavior. New York: Harper and Row, 143 pp. One of several short paperbacks offering a quick and somewhat superficial introduction to the field of behavior; these books are useful in mini-courses and in sections of a broader course, but usually are not in themselves sufficient for a full course.

Wallace, R. A. 1973. The Ecology and Evolution of Animal Behavior. Pacific Palisades, Cal.: Goodyear, 348 pp. A new general introduction to the field of behavior; in paperback, it would be a good buy.

B. Topical References; books offering depth in specific topics

1. Series publications

Series' published by Academic Press, New York; in depth presentations of recent advances.

Advances in the Study of Behavior. Ed. by D. S. Lehrman, J. S. Rosenblatt, R. A. Hinde and E. Shaw. Vol. 1, 1965; Vol. 2, 1969; Vol. 3, 1970; Vol. 4, 1972; Vol. 5, 1974.

Behavior of Non-Human Primates. Ed. by A. M. Schrier and F. Stollnitz. Vol. 1, 1965; Vol. 2, 1965; Vol. 3, 1971; Vol. 4, 1971.

Primate Behavior. Developments in Field and Laboratory Research. Ed. by L. A. Rosenblum. Vol. 1, 1970; Vol. 2, 1971 ; Vol. 3, 1974 ; Vol. 4, 1975.

Benchmark Papers in Animal Behavior, published by Dowden, Hutchinson and Ross, Stroudsburg, Pa. Each volume contains reprintings of the significant papers in a topic area; treatment of the topic is often historical.

Vol. 1. Carter, C. S., (ed.). 1974. Hormones and Sexual Behavior. 362 pp.

Vol. 2. Stokes, A. W., (ed.). 1974. Territory. 398 pp.

Vol. 3. Schein, M. W., (ed.). 1975. Social Hierarchy and Dominance. 401 pp.

Volumes currently in press:

Collias, N. E. and Collias, E. C., (eds.). 1976. External Construction by Animals.

Porges, S. W. and Cole, M. G. H. (eds.). 1976. Psychophysiology.

Hess, E. H. (ed.). 1976. Imprinting.

Muller-Schwarze, D. (ed.). 1976. Play.

Silver, R. (ed.). 1976. Parental Behavior in Birds.

2. Books of defined scope

Hafez, E. S. E. (ed.) 1969. The Behaviour of Domestic Animals. 2nd Ed., London: Bailliere, Tindall and Cassell, 647 pp.

A good reference book for the behavior of the domestic

animals so often used in our various laboratory exercises.

Sebeok, T. A. (ed.) 1968. Animal Communication. Bloomington, Ind.: Indiana University Press, 686 pp. A compendium of research in animal communication up to the late sixties; needs updating.

There are also available now many excellent treatises on individual animal species. Most of these are very readable and of interest to the non-specialist as well as providing much information to the specialist. There are too many to list individually, but I must mention the series put out by the University of Chicago Press; this series includes such treasures as The Spotted Hyena by Hans Kruuk, Mountain Sheep by Valerius Geist, and The Serengeti Lion by George Schaller. Other outstanding Chicago books include Social Organization of Hamadryas Baboons by Hans Kummer, Baboon Ecology by Stuart and Jeanne Altmann, and a host of others.

Two excellent books recently put out by the Belknap Press of Harvard University Press deserve especial mention: The Social Behavior of the Bees by C. D. Michener and The Insect Societies by E. O. Wilson. Both books deal heavily with the evolution of social behavior in insects, with Michener concentrating on the bees (some 20,000 species) and Wilson treating sociobiology more broadly.

C. Journals

1. Of immediate pertinance to biosociology

Animal Behaviour. The official publication outlet of the (American) Animal Behavior Society and the (British) Association for the Study of Animal Behaviour; published by Bailliere Tindall, London. Mostly shorter research

articles emphasizing the biological approach; occasional reviews; all articles are in English.

Behaviour. Published in the Netherlands by E. J. Brill, Leiden. Usually longer research articles reflecting an evolutionary approach to behavior; articles are in English, French, German or Dutch, with a summary in another language.

Zeitschrift für Tierpsychology. Published in Germany by Verlag Paul Paray. Research articles, both long and short reflect an evolutionary approach to behavior. Articles are generally in German, but some are in English or French; English summaries are usually available.

Journal of Comparative and Physiological Psychology. Published by the American Psychological Association. Generally shorter research articles reflecting the approach characteristic of experimental psychologists. Until recently, articles were heavily physiological but an increased amount of comparative work is now planned. All articles are in English.

2. Journals that often contain articles pertinent to biosociology

Animal Learning and Behavior. The Psychonomic Society.

Applied Animal Ethology. Elsevier.

Auk. The American Ornithological Association.

Copiea. The American Society of Ichthyology and Herpetology.

Hormones and Behavior. Academic Press.

Journal of Mammalogy. American Society of Mammalogists.

Social Biology.

Sociometry.

Wilson Bulletin. Wilson Ornithological Association.

3. Scientific American, in a class by itself; often contains at least one behavioral or biosociological article per issue.

D. Films

It is impossible to list all the films presently available that deal with some aspect of biosociology. New films appear on the scene virtually every week and it is a significant chore just to preview them, let alone gather the details on availability, price, etc. My own tendency has been to lean heavily on the Psychological Cinema Register (PCR) of the Pennsylvania State University Audio-Visual Aids Library (University Park, Pa., 16802); they keep pretty well on top of the behavioral films and have an efficient distribution system (within the continental U.S.) at fair rental costs. Most of the films listed below are available for rent and/or purchase from PCR; catalogue numbers are included.

Following is a list of selected films that I find especially useful in teaching biosociology. Some are quite old and others are brand new; they all are useful as illustrations of particular aspects of the field.

Albatross: good study of social behavior of the Laysan albatross during the breeding season; of especial interest is the formation of lifetime pair bonds. PCR, #40117

Animals in Amboseli: exceptional film of the cinema verité type; narration is minimal and no "explanations" are

offered; shows intra- and inter-specific interactions, primarily around a water-hole. There is so much in this film that it should be viewed several times; I use it at least twice, once at the beginning of the semester and again at the end. PCR, #20773

Baboon Behavior. PCR-2107K

Dynamics of Male Dominance. PCR, #31292

These two films are part of a series of films on the behavior and ecology of Anubis baboons. The first is a good introduction to the baboons in their natural setting and defines the general social organization of the troop. The second analyses the central hierarchy and its function in maintaining social stability. These films are now classics, having set a pattern and high standard for a number of primate films that followed.

Behavior and Ecology of Coral Reef Fishes. A recent film that especially ties social organization to feeding habits of different species of Butterfly fish. Some coral grazers establish defended territories around particular coral heads, while others graze more widely over a "home-range" area; in both cases, pairing is common and continuous "checking" of the partner is readily observed. Closely related species feed on plankton near the surface and aggregate in large schools; established pairs are not evident in these aggregates. University of Hawaii

Bleeading Hearts and Bonebreakers. An interesting account, T.V. style, of Gelada baboons (the bleeding hearts) and Lammergeyer birds (the bonebreakers) in Ethiopa; a relaxing film that entertains more than challenges. PCR,#40116

Dances of the Bees. This is a golden oldie that still has its uses despite the current controversy over the interpretation of the bee dance. The scenes are clear, the film is explicit, and it "works": we can translate the dance into food source locations. PCR-103

Ecology and Behavior of the Patas Monkey. Rockefeller Univ.

Ecology and Behavior of Vervet Monkeys. Rockefeller Univ.

Mountain Gorilla. PCR-2141K

Monkeys of Mysore. PCR, #20813

Rhesus Monkeys of the Santiago Island. PCR, #30958

There are now a number of primate natural history films available; these are some that I find quite useful, if only to illustrate the diversity of organizational patterns among the different primate species.

Evolution of Nests of the Weaverbird.

Life in a Weaverbird Colony.

Trace the evolution of nest construction, from simple platform cups to elaborately woven masterpieces in this interesting family of birds; includes scenes of huge colony nests and illustrates social interactions within and between breeding pairs. Univ. of California

Jungle Fowl in India and Ceylon. PCR, #10556

Red Jungle Fowl in Thailand. PCR, #10557

Useful because of the taxonomic proximity of Jungle Fowl to our domestic chickens; shows the social interrelationships between individuals and small groups.

Mallee Fowl. CRSO, Australia

Spawning in African Mouthbreeding Fish. PCR-2185K

Two good examples of very different types of parental behavior. The Mallee fowl spends a good part of the year tending to the mound nest but has nothing to do with the young after hatching; the African mouthbreeding fish broods the young in its mouth until such time when the young can fend for themselves.

Nature and Development of Affection. PCR-116K

Rock-a-Bye Baby. Time-Life Films

Both films deal with parent-young relationships, chiefly in primates. The "Nature and Development" film is by now an old classic showing Harlow's work with surrogate-reared Rhesus monkeys; the "Rock-a-Bye" film is much more recent and includes humans in its coverage.

Stimuli Releasing Sexual Behavior in Domestic Turkeys. PCR-114K

Courtship Behavior of the Queen Butterfly. PCR-2123K

Good demonstrations of the chain sequence of behaviors leading to successful mating; the stimuli involved in each step of the sequence are elucidated, and the importance of intimate communication is well illustrated.

Animal Communication. Time-Life Films

Use of Sign Language by Chimpanzees. Univ. of Nevada, Reno

The first film, "Animal Communication" takes a broad and somewhat superficial look at signals and communication in the animal world; the film is fairly elementary and unchallenging, but it contains a number of otherwise hard-to-get sequences. The "Use of Sign Language" film is new and very exciting; it is the first of what promises to be a most important series depicting the use of a human language by chimpanzees.

Social Reactions in Imprinted Ducklings. PCR-2180K

There are several "imprinting" films currently available, but I prefer this one because of its emphasis on an experimental approach. Ducklings are imprinted to a plastic milk bottle mounted on a toy electric train, and can control the extent of subsequent exposure by means of a readily available key.

Territorial Behavior in Uganda Kob. Smithsonian Inst.

A good example of a "lek" type mating arrangement. Males establish small breeding arenas which they defend against competing males; estrous females enter the arenas and are mated following a brief courtship interplay.

VII. STUDENT PROJECTS AND LABORATORY EXERCISES

In this section, I should like to offer some examples of biosociological exercises and projects that can readily be carried out in the classroom. This collection is intended to supplement a more extensive collection of exercises presented in Animal Behavior in Laboratory and Field edited by Price and Stokes (1975). (Some good biosociological exercises were dropped from the present second edition, but unfortunately the first edition of this handy manual is now no longer available).

The first part of this section is given over to exercises that I have used (with generally successful results) over the past years; they are therefore built around the animals and facilities available in my laboratory. However, in many cases other species of animals can be used, and sometimes not necessarily closely related species. Of course, many variations of procedures can be introduced to expand upon or simplify the classroom exercise, and individual students often are intrigued enough by one or more of the classroom exercises to expand it into an individualized term project.

The second part of this section includes some project reports and classroom exercises contributed by former students of mine and previous participants in Chatauqua Biosociology courses; they are presented here in order to illustrate the diversity of interesting, challenging, stimulating and meaningful ideas that can be pursued in a Biosociology course or in the biosociological component of an existing course.

A. Some Classroom Exercises

1. An Inventory of Behavior

a) Handout to students

This is an exercise in naturalistic observation, designed to acquaint you with some techniques of behavioral observations. An examination of the data obtained from naturalistic observations often reveals relationships between behavioral acts, or between the environment and the organism, that are otherwise obscured. In the course of a unit of time, the individual performs many behavioral acts. Some of these are completely individual acts while others are performed in conjunction with or as a result of being in a social group. For example, a cow may walk along a defined path (an individual act) but the act of walking along this particular path may be governed by the actions of the herd as a group: the entire herd may be moving along the defined path and the individual cow may be acting as a member of the group. Thus, we need to know not only what an individual does at any given time, but also what the group as a whole is doing at the same time. With such information at hand, we may eventually be able to determine the effect of the individual on the group's behavior and the effect of the group on the individual's behavior.

It is extremely difficult to simultaneously observe an individual and the group, especially if one is dealing with an unfamiliar species for the first time. There are at least two ways of getting around this problem: the first entails making many observations, sometimes concentrating on the group and sometimes on an individual; the second method uses a team to make the observations. We will use the second method, since the amount of time required for the first method is not available to us;

teams will consist of at least two people.

The efficient functioning of a team depends upon a high degree of coordination among team members. Tasks should be well defined and assigned in advance of the observation period. One team member should observe the group as a whole and one or more should observe individuals. In the interest of consistency among the various teams, please keep your data on a minute-by-minute basis. Later, these raw data may by lumped into larger time blocks for analyses.

Our problem in this exercise is two-fold: we should like to make an inventory of the various behavioral acts carried out by the individual or the group, and we should also like to have an estimate of how frequently these acts might be performed. Since only two lab periods can be devoted to the exercise, we have no way of relating the levels of activity to specific times of day. However, you should bear in mind that time of day is often critically important to behavioral observations: little "sleeping" or "roosting" behavior will be noted after sunrise, and very little "feeding", "running", etc., will be observed after sunset. Other environmental conditions existing at the time of observation should also be noted, wherever possible. Observations recorded on a cloudy, cold October morning will reveal somewhat different behaviors than observations recorded on a hot, sunny July afternoon. All these details are important in assessing your results, or in compiling your data at some later date. Incidentally, the date of your observations is important if for no other reason than it gives a clue as to the general climate at the time of the observations: you can always go back to weather bureau records for

climatic data for that day.

When dealing with an unfamiliar species for the first time, it pays to spend a certain amount of time just observing and listing the various behaviors. When a sufficient number of acts are listed so that few new ones appear, then you are ready to begin the observations on a time basis. The initial untimed observation period serves two other functions: (1) it allows time for the animals to accustom themselves to the presence of observers and so to resume normal activities; (2) it allows for agreement to be reached among team members as to what to call a particular behavioral act. Such agreement is critical to the proper functioning of the team.

At the end of the pre-observation period, you may want to make up a raw data table so that acts can be quickly recorded. Such a table might have the behaviors in columns across the top, and "time" in rows along the side. Or you might prefer to simply list the times along the side and note the behaviors as they occur. The latter method eliminates the possibility of marking a behavior in the wrong column, but it makes necessary some sort of shorthand: thus, "23T/56" means "animal #23 threatened animal #56, and #56 retreated", or "23/56F" means that the encounter was a fight, and #23 won. Similarly, "23 & 56F" might mean that the fight was indecisive. You are left to your own ingenuity to devise other shorthand symbols (for trough-feeding, drinking, dusting, walking, preening, standing, feather-fluffing, tidbitting, crowing, cackling, running, sitting-on-the-ground, roosting-on-a-perch, etc.) but make sure your system allows for error-free translation into English.

Observations of individual animals and observations of the group as a whole will be made. Observations of individuals should be recorded in terms of everything the individual does during each one minute interval of the observation period. From these data we can make estimates of the percentage of time an individual engages in any activity during the daylight hours.

Ideally, observations of the activities of the group should be conducted in the same manner. However, this method leads to many complications both in recording and interpreting the data. To simplify this situation a sampling technique will be used. In this method the observations are expressed in terms of the number of individuals involved in an activity during the last 5 seconds of each one minute observation period. For example at the end of the first minute 4 birds were eating, 6 were sitting, 10 were standing, 2 were dusting and 1 was drinking. A similar observation would be made at the end of each successive minute. When using the sampling technique one should bear in mind that the accuracy of the observation depends on the assumption that the sample truly represents the whole period, i.e., that the activities of the group during the sample period are the same as the activities of the group at any other time of day. To the extent that this assumption is inaccurate, the data are inaccurate.

Data of this kind may yield clues as to how the activity of one bird affects another. For example if 6 to 10 birds, not just one, were seen eating at each observation period, one might suggest that feeding by some birds tends to engender feeding by others.

At the conclusion of the observation period, we will return to the laboratory to permit each team to assemble its data and draw whatever conclusions possible from the data. In writing up this report you might find it helpful to represent the results in terms of one or more histograms.

Background reading (in addition to your text):

The following chapters in The Behaviour of Domestic Animals, edited by E. S. E. Hafez, 2nd edition, 1969. Bailliere, Tindall & Cassell, London.

Guhl, A. M., Chapter 5. The social environment and behaviour.

Guhl, A. M. and G. L. Fischer, Chapter 16. The behaviour of chickens.

Hale, E. B., W. M. Schleidt and M. W. Schein, Chapter 17, The behaviour of turkeys.

Scott, J. P., Chapter 1. Introduction to animal behaviour.

1.

b) Note to teachers

Obviously this exercise can, with very little modification, be carried out with any available species. The handout was originally written with a number of small (10-15 bird) chicken pens in mind, but I have also successfully used established groups of Japanese quail in large laboratory cages, aquaria containing one (or as a most interesting variant, two or more) species of fish, herds of cows and flocks of sheep in and out of the barn, ants outside our laboratory window as well as flies on the window, and the like. The only equipment needed for this exercise, besides the animals, is paper, pencil and a watch; the more time available, the better the results. On one occasion I listed the species we had available for observation and offered the students free choice of these or anything else they wished to observe; one ingenious pair carefully observed and inventoried the behaviors of their classmates.

A similar type of exercise is very well presented in the beginning section of the Price and Stokes manual.

2. The Behavior of Bees

a) Handout to students

A honeybee (Apis mellifera) colony serves as an excellent example of a closely knit, highly stereotyped, and usually efficient type of insect society. Much like an individual organism, the colony maintains itself and grows under favorable conditions, reacts as a unit to various fluctuations in the environment, defends itself against other colonies, and reproduces when conditions are suitable. The efficient functioning of a colony depends upon a high degree of specialization on the part of the individuals making up the colony. Each individual performs a specific share of the total activities needed for survival so that there is complete interdependence of individuals upon each other. Such specialization is characteristic of the social insects.

A normal colony of honeybees contains a single fertile female (the queen), several hundred males (drones), and several thousand sterile female workers. The queen's sole duty in the colony is to lay eggs. She is fertilized during a courtship flight just prior to the establishment of the colony, and thereafter does not mate again. She produces tens of thousands of eggs during the several years of her lifetime, and depends upon the workers for food and care.

The drones' sole function is to mate with virgin queens during courtship flights. Since they cannot forage for themselves, they are fed by the workers in the hive. They contribute nothing to the maintenance of the colony, and seem to be more or less merely tolerated when conditions in the hive are satisfactory. However, during periods of food shortages

or environmental stress, tne drones are killed or forced out of the hive to starve or freeze. In the summer, the average life span of the drone is about 6 to 8 weeks, but some may overwinter in queenless (disorganized) colonies.

The worker bees are females, but lack the fully developed reproductive organs of the queen. Workers perform all the labors of the hive in a fairly definite order according to age; following is the general schedule of duties performed:

Age (days)

1-3 Janitor: cleaning old cells, removing and discarding debris and dead bees;

3-10 Nurse: caring for hatching eggs and larvae in cells;

10-16 Builder: repairing broken cells, building new cells;

16-20 Relayer: relay pollen, nectar and water from foragers to queen and to nurse bees;

20-21 Guard: protect the hive from intrusion by other bees;

21- Forager: collect nectar, pollen and water from the field and bring it to the relayer bees.

Workers last about 8 weeks in the summertime, when they are active, and several months in the winter, when they are relatively inactive.

Observe a glass-sided demonstration hive. See if you can identify the queen (whose body is much longer than that of an ordinary worker), and drones (who are larger in all proportions than the workers). Find and distinguish between cells filled with brood and honey; note their distribution in the comb. Place the back of your hand directly over the

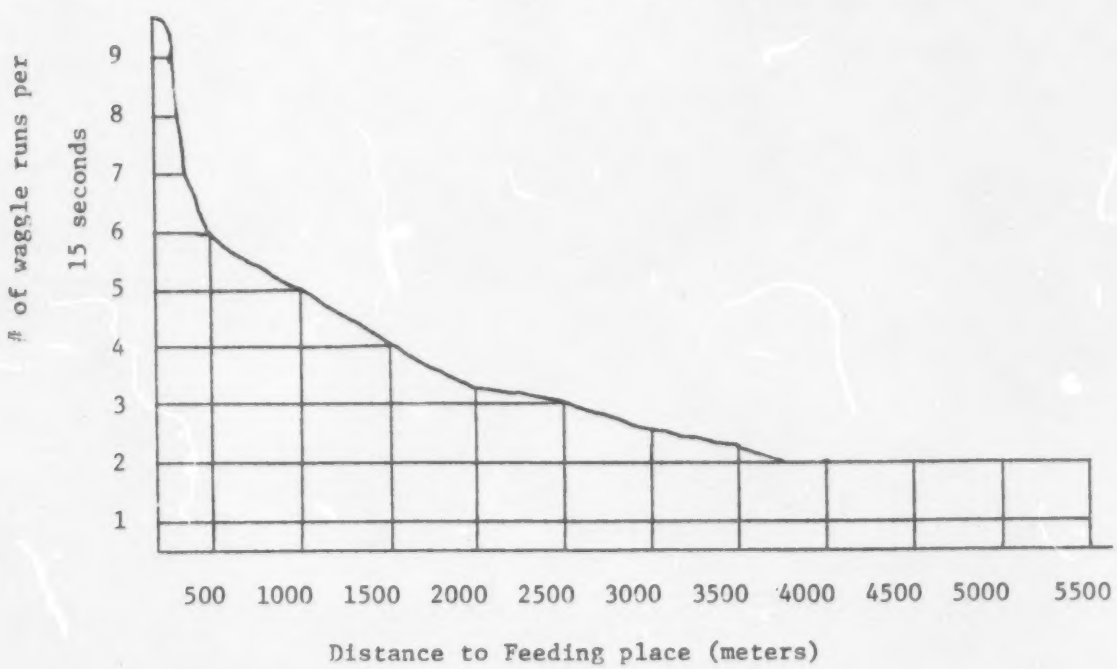
brood chamber. Try the same with your hand over the honey or some other region of the comb. Note the difference in temperature. With the exception of being caught too far from the hive at dusk and thus having to spend a night out, bees lead remarkably homeothermic lives.

Observe a few bees fanning in the entrance to the hive. They are blowing air out of the hive; note that they face away from the entrance. Now look for workers that are sitting over the combs and evaporating moisture by fanning with their wings. What stimulus does a bee use as a clue to the position of the hive entrance in order to direct her stream of air at it? You can very nicely show that it is light by shining an artificial light through the glass walls of the hive (avoid overheating) and observing that the bees fanning at the entrance now direct their fanning at the light. Move the light around and illuminate parts of the whole bottom of the hive and you can get bees fanning at each other, a useless net result to them.

The main part of this laboratory is concerned with a study of the communication of food sources in honeybees. To do this we will divide the class into several groups; two members of each group will go out to feeding stations that have been set up nearby. Those going to feeding stations should try to remain as oblivious as possible to the locations of stations other than the one to which they are assigned. One person is to paint a spot on the thorax of all bees visiting his station. (Each station has a different color associated with it.) The other person notes the number of bees feeding at the station per minute.

Those at the hives should try to decipher the dances of returning bees and on the basis of their interpretation plot the position of as many feeding stations as they can on topographic maps. Having done this they can proceed to one of the feeding stations. If the station is correctly located the finder should take over the records and painting duties of the person at that table who then returns to the hives to take a turn at finding some other feeding station. In the event that you are replaced by someone from the hives just after you yourself have come from the hive simply return to the hive and try your skill again at locating another feeding table.

A final note. Those back at the hive should make careful observations of bees following a dancing bee. Particularly, note where they go after leaving a dance which they have been energetically following.



Suggested reading:

Clarke, W. W. Jr., and Anderson, E. J., Pennsylvania Beekeeping. circ. 472, P.S.U. Coll. Agr. Extension Serv.

von Frisch, K., The Dancing Bees, Harcourt Brace & Co., New York.

Lindauer, M., Communication Among Social Bees, Harvard University Press, Cambridge, Mss., 1961.

Ribbands, C. R., The Behaviour and Social Life of Honeybees. Bee Research Assn., Ltd., London, 1953, reprinted by Dover Press, New York, 1965.

2.

b) Note to teachers

This excellent exercise was originally prepared a number of years ago by Dr. Roger Payne, then a student at Tufts University. It does require some elaborate preparations as well as established observational beehives. Students that are allergic to bee venom should of course not participate in this exercise, although the probability of getting stung in a proper observational set-up is minimal. We used home-made single-frame observational hives that we set up in a shed near the University flower gardens. (Two and three-frame observational hives are available commercially, especially from biological supply houses.) Our hives opened only to the outside, so that students could observe the bees in the safety and protection (if not comfort) of the shed. We have also maintained observational hives in heated buildings (again, with openings only to the outside), in which case the colonies readily survive through the winter months and provide opportunities for new sets of observations (such as behavioral thermo-regulation in the colony).

For the purposes of this exercise, it is necessary to set up feeding stations for the bees a number of days ahead of time. Our feeding stations consisted of small plywood platforms (15 cm square) attached to the tops of tall wooden stakes; a dish of concentrated sugar-water sat on each platform. It often proved necessary at the outset to heavily scent the sugar-water (anise oil or something like that) to initially attract the bees and/or to locate the station just about at the entrance of the hive (remember, we were competing with the nearby University flower garden). However, once the bees started to feed at a station, we found we could move it out by several-meter stages without losing the bees. Eventually, perhaps in a couple of days, stations were established as far away as half a mile or so from the hive.

Stations were also sometimes color-coded by means of a piece of colored paper sitting under the dish of syrup. Changing around the colors of a group of feeding stations provides for another set of interesting experiments.

Marking the bees at the feeding station presents no real problem, since the bees seem to devote virtually exclusive attention to the sugar-water. The first few bees marked by students will undoubtedly end up bathed in paint, but with a fine camel's hair brush, a relatively stable hand and just a modicum of experience, permanent marks can be adroitly placed on the back of the thorax without touching either the wings or the head. Properly marked bees seem to survive as well as their unmarked sisters, and a marking persists throughout the lifetime of the bee.

Other equipment needed for this exercise includes protractors (with simple plumb bobs) to measure the angle of the waggle runs with respect to the vertical, stop-watches to time the number of turns, some compasses for plotting directions on the maps, and topographical maps of the area (which in fact can be simple mimeographed sketches).

Despite great initial trepidations and skepticism, students find to their utter surprise that the technique works and they can accurately plot feeding stations merely by observing and measuring the dances of the bees in the hive. The bee experiment usually turns out to be one of the more popular exercises of the semester and is therefore well worth the set-up efforts.

3. Parental Behavior in Chickens

a) Handout to students

The purpose of this exercise is to examine several aspects of the parent-young social bond. A number of hens have been isolated with several eggs in warm, quiet, relatively dark compartments. Under these conditions, hens with favorable genetic makeup become "broody", i.e., they stop laying eggs and sit in a nest on the eggs. If the eggs are allowed to hatch, or if young chicks are introduced, the hens exhibit parental behavior and protect the young. If a hen is not completely broody at the time the young are introduced, it at best ignores, or more commonly kills, the chicks. Continued introduction of chicks will in time make a hen broody.

We will observe the establishment of the parent-young bond by introducing several newly-hatched chicks to each hen during the first laboratory session. The hens will be checked daily during the week, and dead chicks replaced with new ones from a stock supply. Note the response of the newly-hatched chicks to the hen, and vice-versa, upon the initial introduction. Do these responses change markedly during the course of the week? What about the responses of the chicks to each other? to people?

The parent-young bond should be firmly established by the following week and several tests of the bond will be performed; note responses of the parent and the chicks at each step:

1) approach and open door to home compartment;

2) capture one of the chicks

3) hold chick in such a way as to <u>avoid</u> having distress calls emitted;

5) borrow several chicks of the same species as yours from another team and introduce them into your compartment (chicks should be color marked for identification).

After the initial tests, two family groups will be released in a large ring for a 15 minute period. Note responses of the hens towards each other and towards the other's chicks. Note also the chicks' responses to their own parent, to the other parent, and to the other group of chicks. What is the spatial arrangement of each family group?

If time permits, a non-broody hen will be placed in the center of the room with a family, and responses of all birds will be noted.

Background reading (in addition to your textbook):

The following chapters in The Behaviour of Domestic Animals, edited by E. S. E. Hafez, 2nd edition, 1969. Bailliere, Tindall & Cassell, London.

Guhl, A. M., Chapter 5. The social environment and behaviour.

Guhl, A. M. and G. L. Fischer, Chapter 16. The behaviour of chickens.

Hale, E. B., W. M. Schleidt and M. W. Schein, Chapter 17. The behaviour of turkeys.

3.

b) Note to teachers

The heavier (meat) breeds of chickens (e.g., White Rocks, Barred Plymouth Rocks, New Hampshires) work very well in this exercise because they can easily be made broody. White Leghorns, on the other hand, have much higher thresholds for parental behavior and are not recommended; if they are all that is available, prepare to extend this two week exercise into a third week and be sure to have a good stock of newly hatched chicks available to "feed" the potential parent. A bird such as the White Rock quickly responds to the warm, quiet compartment and readily accepts the chicks. Be prepared, though, for some potential parents to viciously attack and kill the first few chicks introduced and then to just as viciously defend the suddenly adopted next few chicks from the intruder's hand.

4. Parental Behavior in Japanese Quail

a) Handout to students

The purpose of this exercise is to examine several aspects of the parent-young social bond.

We will observe the establishment of this bond by introducing various numbers of newly hatched quail chicks to several Japanese quail hens, some of which have previously raised a brood and some of which are naive. Note the initial responses of the chicks to the hen and vice-versa. Do experienced hens differ from naive ones?

The hens should be observed often during the week. Note any changes in their behavior and that of the chicks toward each other and humans. Note data and condition of dead chicks.

The parent-young bond should be established within a week and several tests of this bond can be performed; note responses of hen and chick at each step:

1) open door to cage and move chicks, one at a time, to test cage; allow to move about briefly;
2) place hen in cage with chicks;
3) place non-broody hen in isolation box behind wire door;
4) remove wire door and release stranger into test cage;
5) remove stranger, capture chicks and place in isolation box behind wire door (if necessary block them from hen's view);
6) release all but one chick;
7) you devise one or more tests.

After the individual tests, two family groups will be released into a large cage for a 15 minute period. (You will probably want to color mark them to make observation easier.) Note the parents' responses to each other and the others' chicks. Also note the chicks' response to each other and the strange female. What is the spatial arrangement?

What aspects of parental behavior are these tests designed to measure? Are there other aspects of parental behavior that might be used? How could they be tested?

From your data, what can you conclude about the role of experience in parental behavior? Would this have significance under natural conditions?

Do you think different results would have been obtained if the hens had reared their own chicks instead of foster chicks? Explain.

Suggested reading:

The following chapters in The Behaviour of Domestic Animals, edited by E. S. E. Hafez, 2nd edition, 1969. Bailliere, Tindall & Cassell, London.

Guhl, A. M., Chapter 5. The social environment and behaviour.

Guhl, A. M. and G. L. Fischer, Chapter 16. The behaviour of chickens.

Hale, E. B., W. M. Schleidt and M. W. Schein, Chapter 17. The behaviour of turkeys.

b) Note to teachers

Shortages of space and facilities forced us to abandon chickens as laboratory animals; we therefore modified Exercise 3 to the present form which uses Japanese quail instead. However, the change in species forced one important change in procedures: since Japanese quail have extremely high thresholds for parental behavior, we cannot make the birds "broody" before introducing the chicks. Thus, mortality among the first batches of introduced chicks is very high and a good stock of chicks hatching over a period of several days will be needed for this experiment. Outright chick killing by the adult usually terminates by the second or third day of introduction, and the shift from attack to mere tolerance to acceptance to active defense can be readily observed and measured.

The number and density of chicks introduced to a potential parent seem to be important variables in this exercise, and students should be encouraged to design experiments around these variables. We have found that broodiness is more quickly established (and chick mortality is significantly lower) if the adult has to cope with 12 to 15 chicks at a time rather than 3 to 5; further, if the chicks and adult are crowded together in a small cage, then parental behavior is more quickly and firmly established.

We have used "experienced" versus "naive" adults as prime variables simply because we usually have such birds around. However, there are many other possible variants that can be introduced into this exercise (e.g., sex of the potential parent; administration of hormones; cross-fostering with other species), depending upon the facilities and time available and interests of the students. We also have hints that birds that were reared by a foster parent have somewhat lower thresholds for parental behavior than others that were reared solely with siblings in a commercial brooder. We have not yet had birds incubated and reared by their true parents.

5. Parental Behavior in Mouthbrooding Fish

a) Handout to students

Many cichlid fish of the genus Tilapia are oral brooders, i.e., after spawning one or both sexes, depending on the species, takes the fertilized eggs into the mouth cavity where they are retained until the eggs have hatched and the young fry have undergone further development. Female T. mossambica carry the eggs and young fry for approximately 10 to 12 days after spawning. After this the young are released but kept under parental supervision for another 5 or 6 days before dispersing. In the case of "danger" during these 5 or 6 days, the female makes some violent movements, moves toward the cluster of young, and assumes a diagonal position with head downward at approximately 10 to 20°. In this position she swims slowly backward, and the young fry swim rapidly toward her and enter her mouth cavity.

In the following series of experiments you will attempt to determine some of the important characteristics of the female's behavior that releases this response in the young and the stimuli that guide the young to the correct area, i.e., the oral cavity.

Using the model of the female, perform the following manipulations and record the young fry's behavior. Each presentation should not occupy more than 3 or 4 minutes, and to reduce habituation to the models an interval of at least 10 minutes should be allowed between tests.

1) enter the model slowly into the water and hold it stationary about 2 inches off bottom;

2) move model slowly about aquarium;

3) move model quickly side to side and then follow this with a slow backward movement of the model;

4) repeat as in 3, only move the model forward instead of backward;

5) repeat as in 3, but hold the model so head end is pointing up 10 to 20°.

Repeat the above procedures with the other models available and perhaps with models of your own design; note especially where on the models the fry congregate.

From the limited experiments performed, can you draw any conclusions as to what behavior on the part of the female releases the returning to the mouth cavity by the fry, and what might be the relevant stimuli directing the fry to the oral cavity? What other factors might be concerned here, and how would you design an experiment to test your hypothesis?

Suggested readings:

Marler, P. and W. Hamilton. 1966. Mechanisms of Animal Behavior. John Wiley and Sons, New York. pp. 305-306.

Baerends, G. P. and J. M. Baerends-Van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. Behaviour Supplement I. pp. 190-201

Russock, H. I. and M. W. Schein. 1974. Effect of early experience and age on initial responsiveness of Tilapia mossambica fry to a maternal model. Animal Learning & Behavior, 2:111-114.

5.

b) Note to teachers

Exercise 5 was designed by Dr. Louis Rigley, Wilkes College (then a graduate student in our laboratory), to provide an alternative to the birds in Exercise 4. It demands a fair collection of adult fish in order to have a sufficient number of broods of young at just the right age for the exercise. The fish are quite hardy and good stocks are maintained with minimal bother; they are usually available in local tropical fish stores. When the adults cooperate, the exercise works very well.

The models mentioned in the handout are attached to long wire handles, thereby permitting movement and manipulation in the tanks. One model is that of an adult female: either a good wooden or clay replica, appropriately marked, or a real female properly preserved (coated with clear plastic). Other two or three dimensional plywood or clay models can be circular, spherical, rectangular, cuboid, ovoid or just irregular and marked in a variety of ways depending upon the ideas presented by the students. Our "standard" model, which is highly effective in attracting fry, is a simple flat grey disc, about 4 cm in diameter, with one or more black dots (2 mm in diameter) painted on the face of the disc.

6. Sexual Behavior in Japanese Quail

a) Handout to students

In common with most complex behaviors, an awareness of the patterns of sexual behavior is critical to studies of the levels of sexual behavior. In addition to the patterns, one must recognize the stimuli releasing the behavior so that test conditions are optimal for each experimental group involved. The object of this exercise is relatively simple: we should like to determine what effect, if any, sexual deprivation has on the expression of male sexual behavior.

In designing an experiment to achieve the objective, we try to control various factors that might render our data uninterpretable. All males in the study are sexually experienced adults, and since all testing will be done at the same time, season, climate, time-of-day, etc., these factors should affect all birds equally.

Males from each of two groups will be used:

Group 1) those that have been with females for at least three weeks prior to the onset of the experiment;

Group 2) those that have been maintained in groups of males for at least three weeks prior to the onset of the experiment.

The males will be released singly into pens of females for a period of time (at least 20 minutes) and the incidence (and perhaps quality) of sexual behavior will be observed. Pens of females will be made available for the study, and one team of four people will be assigned to each pen. At the end of the observation period, data from the four teams will be pooled.

It should be apparent that a design of this type will yield a comparison between group 1 males (not-sexually-deprived controls) and group 2 males (sexually-deprived experimentals). On the basis of your experience to date with Japanese quail, perhaps supplemented by some pilot work, can you determine how many birds you might need in each group to get meaningful data?

During the course of your observations, note carefully the patterns of male and female sexual behavior; a written description to be included in yor report would certainly be in order. Is there much variability in patterns between different males? between successive matings by same male? between patterns exhibited by different females? Can you make some educated guesses as to the stimuli releasing various components of male sexual patterns of the two sexes? Do your observations tend to confirm published reports of sexual behavior patterns of chickens? of stimulus components?

Background reading:

The following chapters in The Behaviour of Domestic Animals, edited by E. S. E. Hafez, 2nd edition, 1969. Bailliere, Tindall & Cassell, London.

Hafez, E. S. E., M. W. Schein and R. Ewbank, Chapter 9. The behaviour of cattle, Section II, pp. 257-270.

Guhl, A. M. and G. L. Fischer, Chapter 16. The behaviour of chickens, Section IX, pp. 536-543.

Hale, E. B., W. M. Schleidt and M. W. Schein, Chapter 17. The behaviour of turkeys, Section III, pp. 561-575.

also

Schein, M. W., M. Diamond and C. S. Carter, 1972. Sexual performance levels of male Japanese quail (Coturnix coturnix japonica). Animal Behaviour, 20:61-67.

Schein, M. W. and C. S. Carter, 1972. Sexual behaviour and novel stimuli in male Japanese quail (Coturnix coturnix japonica). Animal Behaviour, 20:383-385.

6.

b) Note to teachers

This exercise was originally developed with chickens but is presently used with quail. Indeed, it is probably readily adaptable to any number of moderately promiscuous species. While the primary variable is sexual deprivation, in fact we use the exercise to familiarize the students with patterns of sexual behavior and to raise questions about the relevant stimuli. Some students then move off into independent work with models to test their hypotheses about the stimulus control of sexual behavior.

7. Sexual Behavior of Japanese Quail (alternative)

a) Handout to students

The sexual response of a male to a female varies with the time since his last exposure to females. That is, levels of sexual behavior are directly affected by the amount of stimulus deprivation experienced by the male. However, the pattern components exhibited by males and females as they progress from initial courtship to completed copulation are not subject to as much variability.

The questions to be answered in this exercise involve quantitative and qualitative measurements of sexual behavior in mature male Japanese quail. We will describe the patterns before your observations begin so that you can recognize them as part of the mating sequence. How do you think different lengths of sexual abstinence may affect the male's courting, neck grabs, and ejaculations and the latencies to each of these actions? Will the patterns change as deprivation is increased? What types of reactions do you expect from the females?

The males to be used are sexually experienced. They have been separated into four treatment groups, receiving 0 (control), 2, 4, or 6 days of sexual deprivation through isolated confinement in small cages among the other colony birds. The females are also mature, sexually experienced, and have been in all-female groups for 3 days.

Each team of observers will test 4 different males, one at a time, each from a different treatment group. Each test is for 15 minutes. Procedures are as follows:

Place the male in the testing cage. After 1-2 minutes of adaptation time, add 1 female. Every 5 minutes replace old female with an unused one. (Each male is allowed 3 females during his test.) Note all courtships (C), neck grabs (G) and ejaculations (E) occurring during each 30-second period. If desired, record post-ejaculation behavior of the male and reactions of the females. Data from all observations should be pooled for the final report, and statistical analyses made if possible.

Describe male and female patterns you observed. Do they always occur in a specific sequence? Are there consistent reactions from both sexes following copulation? Do the males alter their activity when a new female is introduced?

Compare class data for number of courtships, neck grabs, and ejaculations in each treatment group. Also compare latencies to the initial court, grab, and ejaculation from one treatment group to another.

When are minimal and maximal levels reached? Where are the significant level shifts? Which amounts of deprivation are most effective in achieving high levels of which behaviors? How might the levels of these behaviors change after much longer deprivation? What problems do you envision in studies of this sort where two animals must interact for the measured patterns to be observed?

The adaptive value of sexual behavior is obvious. How might your results fit into the natural life style of wild coturnix quail?

Suggested reading:

The following chapters in The Behaviour of Domestic Animals, edited by E. S. E. Hafez, 2nd edition, 1969. Bailliere, Tindall & Cassell, London.

Hafez, E. S. E., M. W. Schein and R. Ewbank, Chapter 9. The behaviour of cattle, Section II, pp. 257-270.

Guhl, A. M. and G. L. Fischer, Chapter 16. The behaviour of chickens, Section IX, pp. 536-543.

Hale, E. B., W. M. Schleidt and M. W. Schein, Chapter 17. The behaviour of turkeys, Section III, pp. 561-575.

also

Schein, M. W., M. Diamond and C. S. Carter, 1972. Sexual performance levels of male Japanese quail (Coturnix coturnix japonica). Animal Behaviour, 20:61-67.

Schein, M. W. and C. S. Carter, 1972. Sexual behaviour and novel stimuli in male Japanese quail (Coturnix coturnix japonica). Animal Behaviour, 20:383-385.

7.

b) Note to teachers

This exercise was developed by Ms. Carol Hunt, a graduate student in our laboratory, to serve as an alternative or as a supplement to Exercise 6. It requires no special equipment other than a stop-watch and often forms the basis for more independent studies by the student.

If it is used as a supplement to Exercise 6, then it is not necessary to describe the patterns of sexual behavior since the students will have observed them earlier. If it is used as an alternative to Exercise 6, then a brief live performance (or even a film clip) can be used to familiarize the students with the patterns of male sexual behavior.

8. Agonistic Behavior

a) Handout to students

This exercise is designed to make evident the "peck-order" social relationship among birds. At the same time, you will have an opportunity to observe the patterns of agonistic interactions among chickens, to quantify the levels of such interactions, and to gain some awareness of the stimuli that might release the behavior.

Agonistic behavior includes threats, challenges and chases, as well as actual physical contact. A fight is an obvious affair, since it includes a battery of concomitant movements and sounds. The winner of a fight is also almost always obvious: its movements and actions are easily distinguished from those of the loser. Chasing and fleeing behaviors need no comment: there is little chance of confusing the chasing animal from its fleeing colleague. (On the other hand, the observation of one animal running will not permit you to judge whether it is running <u>after</u> or <u>from</u> something; it takes at least two to make a chase.)

Perhaps the most subtle components of agonistic interactions are the threats. The victor in such interactions is just as victorious as if it had soundly whipped the loser. In many species, threats, submission, and greeting movements have evolved into rather stereotyped or ritualistic movements, and it often requires perceptive observation of the species before the code is understood. For example, by recognizing the social signals and responding accordingly, researchers have been able to successfully interact socially with untamed wolves. In this case, the position of the wolf's ears indicate whether the animal will attack or will submit.

If one were to examine the record of a series of agonistic interactions in an established group over a period of time, two things would be evident: 1) there is a consistent and stable relationship existing between any two animals in the group; 2) the number of interactions per unit time is relatively low. With respect to the first item, if the relationships between individuals were plotted, an order of ranking would emerge revealing that animal A dominates all the animals in the group, animal B dominates all except A, animal C dominates all except A and B, and so forth until the last animal, W, is reached. The unfortunate W is subordinate to all the others in the group, and dominates none. The rank order as described here goes under several names; peck-order, bunt-order (cattle), dominance hierarchy, social hierarchy, etc. Deviations from the just described straight-line hierarchy are not uncommon: A may dominate B who dominates C who dominates A. Again, A may dominate B and C, but the dominant-subordinate relationship between B and C may not be clearly established, yet both B and C dominate D, E, F, etc. In many groups, dominance hierarchies are stable for long periods of time (years, in cows), while in others (male turkeys during breeding season) the order may change from week to week. Flocks of hens are relatively stable, the order remaining unchanged for weeks or months while flocks of roosers are less stable.

The second point mentioned above, that the number of interactions is relatively low, is related to the fact that the net result of the establishment of a dominance hierarchy is to minimize agonistic encounters in the group. Once the hierarchy is developed and every individual knows its place, the stimulus conditions evoking further fighting are reduced or

eliminated. Dominant animals may threaten, but subordinate individuals either avoid or submit rather than challenge back. Thus, stimuli evoking further threats or challenges are reduced or absent.

For the purpose of this experiment, the level of agonistic interactions has been enhanced by the simple expedient of separating and isolating the test animals for a period of time. In order to avoid giving any bird an undue advantage, they should be released simultaneously in the neutral test arena. You should be able to note a gradual and significant change in the level of various components of agonistic behavior, as your test birds establish dominance relationships among themselves. At the end of the observation period, you should also be able to make a first approximation of the rank order of your birds. Is the rank order related to weight? to size of comb? to total body length? to amount of crowding? to any other obvious morphological features?

Note: A simple method for assembling a series of observations into rank order is to make a preliminary table as follows:

A/B - 0
A/C - 3
A/D - 7
B/A - 5
B/C - 4
B/D - 2
C/A - 0
C/B - 0
C/D - 11
D/A - 0
D/B - 0
D/C - 0

Data on encounters between birds can then be assembled in the following fashion:

LOSSES

WINS	A	B	C	D
A		0	3	7
B	5		4	2
C	0	0		11
D	0	0	0	

Then rearrange the table listing birds who have won most first and if the peck order is perfect, all losses will be above the diagonal. Though this is rarely the case, a trend should be evident.

Suggested reading:

Guhl, A. M. and G. L. Fischer, 1969. The behaviour of chickens. In: The Behaviour of Domestic Animals, E. S. E. Hafez, editor; 2nd edition. Bailliere, Tindall & Cassell, London.

Schein, M. W. (ed.), 1975. Social Hierarchy and Dominance. Dowden, Hutchinson & Ross, Stroudsburg, Pa.

b) Note to teachers

This exercise can be carried out with a number of conveniently available hierarchial species. Prior preparation requires social isolation of the animals to be used in the exercise and arrangements for proper encounter areas. It is also important to ensure that each animal is readily and clearly identifiable. Large colored numbered plastic shoulder bands, available from most poultry supply houses, are very useful. If paint marks are to be applied to chickens, avoid the color red since it seems to invite pecking by others. The only other pieces of equipment needed for this exercise are paper, pencil and a watch.

The use of non-hierarchial species calls for significant modifications of the exercise. Japanese quail are essentially non-hierarchial and, further, levels of agonistic behavior are low in these animals. Socially deprived males are more likely to sexually mount each other than to fight. Students readily note who mounts whom and assume that mount order (if any emerges) is the same as dominance order; the assumption is unwarranted. Socially deprived Japanese quail do little if any fighting when assembled in an arena. However, following copulations and especially after a few repeated matings, some females viciously attack, chase and otherwise harass the males.

9. Effects of Androgen on the Behavior of Chicks

a) Handout to students

Androgens are male sex hormones produced mainly in the male gonad. Their profound effects on behavior can be readily demonstrated by several means, chief among which are to remove the source of the hormones in an adult male, or to introduce an androgen to an animal that has no source of its own (such as a juvenile). In both cases, one looks for changes in behavior as the endogenous hormone is dissipated (castration of adult) or as the administered hormone is utilized (injection of immature). When the behaviors have been stabilized, the procedure is often reversed: hormones are administered to the castrate or withdrawn from the juvenile. Since the animals then revert back to their original form and levels of behavior, the role of the hormone has been clearly established. It is interesting to note that with a hormonally mediated behavior, some optimum level usually exists whereby further increases in the quantity of hormone do not result in increases in the amount of behavior exhibited.

Whereas neural modification of behavior is fast and virtually instantaneous, chemical modification is much slower and requires hours or days to show effects. Consequently, several days are required to demonstrate the full effects of the hormone administration. We will administer an androgen, testosterone propionate, to young chicks and/or Japanese quail for a number of days and observe its effects during the following laboratory session. Teams of observers will be assigned an experimental and a control group of birds, about 10 birds per group. The experimental animals will be injected daily, as follows:

Chicks: 0.1 mg. (0.02 ml) testosterone propionate, 7 days;

Quail: 0.05 mg.(0.01 ml) testosterone propionate, 3 days.*

Control chicks will be injected with sesame oil following the same schedule and dosage as experimentals.

At the end of the period of injections, the groups will be compared in tersm of general morphology (comb size, spurs, feathering), vocalizations (crows and distress calls), and sexual and/or aggressive behaviors. The following series of tests should be performed and the data used to compare the experimental and control groups:

1) measure the comb size(chickens), spurs (chickens), and feathering condition (chickens and quail) of each bird;
2) record the total number of distress calls and crows from each group for a 10 minute period;
3) isolate an experimental bird in a test cage and record the frequency and types of vocallization during a 5 minute period; repeat several times, using both experimental and control birds;
4) pick up and hold an injected bird for one minute, and record its calls; repeat with control bird.

* If enough quail are available, one team will inject 0.1 mg (0.02 ml) testosterone propionate per day for 3 days. Responses of these doubly-dosed birds will be compared to the other groups receiving only half the quantity or hormone.

Suggested readings:

Collias, N. E. 1956. Hormones and behavior with special reference to birds and the mechanisms of hormone action. In: A Symposium on Steroid Hormones, E. S. Gordon, editor. pp. 277-329. Univ. of Wisconsin Press, Madison.

Marler, P., M. Kreith and E. Willis. 1960. An analysis of testosterone-induced crowing in young domestic cockerels. Animal Behaviour, 10:48-54.

9.

b) Note to teachers

This exercise was originally developed by Dr. E.B. Hale, The Pennsylvania State University, and it is one of our old standbys. Inclusion of Japanese quail came later, and now we use nothing but quail in our laboratory. However, it is not an exercise that can be easily adopted to non-precocial birds nor to mammals: neonatal administration of sex hormones to mammals often has profound and permanent effects on physiological development and subsequent behavior.

Injection of birds in this study can start as early as a half-day posthatching; the earlier the injections start, the sooner will results be apparent. We have injected quail shortly (hours) after hatching and observed them crowing before reaching 24 hours of age. Since the chicks used in this exercise are unsexed, an important piece of information (the sex of the bird) must await either post-experiment autopsy or maturation of the survivors. Students are usually surprised to discover that the chick that crowed so avidly and behaved so masculinely subsequently turned out to be a genetic female.

10. Social Integration in Birds

a) Handout to students

For many species, social experiences early in life are necessary to permit the normal expression of social behavior throughout an individual's lifetime. Continuous mingling and interacting with siblings and/or with parent(s) from birth or hatching onward provides the individual with the requisite social experience throughout the critical time period. The quality and intensity of socialization necessary to normal development have not been generally studied, but we do have information on the critical posture of socialization in several species of birds (and at least one mammal, the dog). In precocious birds, the most sensitive portion of the critical period generally lasts but a few hours and occurs sometime within the first 2 days after hatching. In this exercise you will observe the effect of social deprivation in early life on subsequent socialization.

The physical distance between two unrestrained individuals of a social species is often an indication of the degree of affinity between the animals. This affords us a convenient index for estimating socialization: if the normal interanimal distance is known, then experimental animals exhibiting greater interindividual distances could be considered to be less cohesive, or less social. Of course, we must bear in mind when interpreting data on interanimal distance that we could be led astray by factors not related to socialization. For example, the clustering of animals (minimum interindividual distances) around a food source may reflect the geographical limits of the food supply rather than the degree of socialization.

A. Procedure

One-week-old domestic chicks or chicks of Coturnix quail will be used in this exercise. One group will have been reared in isolation cubicles so that no individual has ever seen any other bird (except perhaps within the first few minutes after hatching). The other group will have been reared as a group, with free and continual interactions with siblings. The class will be divided into teams of three people, with each team assigned three birds as follows:

Team	Experimental grouping
A	1. Three group-reared birds
B	2. Two group-reared birds plus one isolate
C	3. One group-reared bird plust two isolates
D	4. Three isolates

Additional observational teams, as available, will replicate team A and team D study groups in order to provide more normal and extreme data. The three birds in each group will be color-coded for identification purposes, and released together into a reasonably large circular enclosure (about 3 meters in diameter) at room temperature. A simple way to make the enclosures is to use a roll of 30 cm wide corrugated cardboard or a properly braced roll of brown wrapping paper. To standardize test conditions remove all food and water for the duration of the observations. This will eliminate grouping in response to some common stimulus, i.e., food and water. Keep the enclosure as circular as possible so that distances between any two birds are not artifacts of a "corner" effect. Each team member will assume responsibility for estimating the distance between a prearranged pair of

birds every 30 seconds for a 25-minute period. (Since there are three birds in each experimental group, three pair interactions are possible.) To permit ready assemblage of data, make your distance estimates in tenths of meters; consider anything less than 10 cm as zero. The observers should remain quiet and motionless to minimize disturbance to the test chicks.

Either during or after your 25-minute observation period make qualitative observations on the birds' behavior.

1. Are there any gross or striking differences in locomotor patterns between the two types of birds?
2. Are there differences in vocalizations? In escape attempts?
3. Do the behaviors change during the course of the 25-minute observation period?

B. Analysis

At the end of the observation period, pool the data for the class. Calculate the mean distance between the three possible pairs of chicks in each experimental grouping.

Are there significant differences in the mean distances between groups? If so, is there a consistent trend in the differences going from group 1 through group 4?

Compare your quantitative and qualitative observations on socialization with socialization in other species, such as rats, dogs, and Rhesus monkeys as reviewed by Denenberg.

If time permits repeat your observations with another species. Can you generalize about the role of social deprivation upon social integration?

What are the trends of the mean distances within groups during the time period of this exercise? Are there differences in trends between groups? On the basis of the within-group tends, can you predict what the mean distances would be in an hour? In a day? In a week?

What would be your prediction about the outcome of this exercise had these birds been adults instead of week-old chicks at the start of the experiment?

Background reading:

Denenberg, V. H., 1962. The effects of early experience. In: The Behaviour of Domestic Animals, E. S. E. Hafez, editor; 2nd edition, pp. 109-138. Bailliere, Tindall & Cassell, London.

McBride, G., 1971. Theories of animal spacing: the role of flight, fight and social distance. In: Behavior and Environment - The Use of Space by Animals and Men, A. H. Esser, editor, pp. 53-69. Plenum Press, New York.

10.

b) Note to teachers

This exercise uses interanimal distance (IAD) to measure sociality (see earlier discussion, pgs. 24-28). It was included in the first edition of Animal Behavior in Laboratory and Field (edited by A.W. Stokes, 1968) which unfortunately is no longer available. The exercise works well with any precocial bird species and probably with precocial mammal species if space and facilities are available.

Some lab preparation is necessary if the exercise is to be successfully carried out. Rearing young birds in isolation can be tricky and anywhere up to 50% or greater mortality should be anticipated. If space and facilities (and time) are available, then a more elaborate design could include the use of two, four and six-week old birds as well (see discussion, pgs. 25-27).

Room and floor temperatures are important, especially with the younger birds: one-week old birds placed on a cold concrete floor are likely to do little except issue distress calls regardless of their social experiences. Also, it is important for the observers to remain as unobtrusive as possible while carrying out the experiment, since they could significantly influence the movement and grouping of the test animals. It often helps to chalk a number of 10 cm lines on the floor of the arena to aid in judging distances between birds. If the chalk lines are spread randomly throughout the arena, then they do not seem to influence the grouping of the chicks.

The chicks should naturally be released simultaneously into the arena and the point of release is of significance. If they are released together in the center, then any movement would increase the IAD; similarly, if they are released as far apart as possible on the perimeter of the arena, then any movement would automatically decrease the IAD. Therefore, the only logical release point is around the perimeter of a circle whose radius is half that of the test arena.

11. Communication and Social Behavior

a) Handout to students

The behavior resulting from the interaction of two animals is a function of the communication between the two; an interpretation of the signals emanating from one of the animals is a prerequisite to the response of the other. The person who flees from a charging bear obviously has interpreted the bear's rapid advance as a sign of iminent peril, even if the bear really has something else in mind. Gross misinterpretations of communicative signals, either interspecific or intraspecific, are generally maladaptive: it would be foolhardy indeed for the person to risk interpreting the bear's charge as parental or courtship behavior.

Communication signals may be perceived by any of the senses, and the proper interpretation of the signal (which governs the response) is often learned by experience. Thus, a browsing deer is put on the alert by the sound of a twig snapping (an environmental signal that sometimes means trouble), and flees at the sight or smell of the predator (a signal that almost always means trouble). However, responses to at least some signals seem to be innate; these responses are evidenced very shortly after birth or hatching, and there is no evidence as yet to indicate that learning or experience modifies the initial response.

A striking example of a presumably innate response to communication signals is shown by newly-hatched domestic ducklings. These birds respond to trains of intermittent calls ("come-come-come-come") with "approach" behavior, and they also respond to the visual signal of a large moving object with "following" behavior (minimizing inter-animal distance). Within a

short time, they learn to associate the calls with the moving object, and thereafter restrict their responses to "calling-moving" objects.

The specific characteristics of the call signal which elicit approach are basically unknown, except that the call must be intermittent and probably should have a sharp or stacatto onset. The specific characteristics of the visual signal are equally vague, except that it should be a large moving object. In the natural situation, such innate responses have high adaptive value: the duckling is most likely to be confronted with its parent rather than some other species. The moving calling parent provides visual and auditory cues to the duckling; as responses to the signals are reinforced (food, warmth, etc.), the duckling soon learns to eliminate "approach" responses to biologically inappropriate objects. The approach response of ducklings to various visual and auditory responses will be demonstrated.

On the other side of the coin, animals generate signals in response to various physiological or environmental cues. The pup separated from its mother whines continually until contact (tactile or at least visual) is restored. Both heredity and experience undoubtedly pay an intertwined role in the generation of signals: initial vocalizations of most animals usually "come with" the animal, but experience teaches it to modify the signal to insure the most appropriate responses.

In the present exercise, we will examine the relationship between group size and the intensity of distress signals. In this case, the number of distress calls per 30 seconds will be used as a measure of intensity. Teams will each be assigned two similar cages, A and B, and six ducklings. The

sides of the cages will be covered with paper so that the ducklings cannot see (and therefore react to) people; small peepholes punched in the paper will permit observation of the birds. At a given signal, one duckling will be placed in cage A while 5 are placed in cage B, and the number of distress calls per 30-second interval will be recorded for a 5-minute period. At the end of 5 minutes, one bird will be removed from cage B and placed in cage A, and the recording will be resumed for another 5 minutes. By repeating the entire process each 5 minutes, we will eventually have 5 birds in cage A and 1 in cage B; thus, data on both ascending and descending group sizes will be available for comparison.

At the end of the experiment, the data from all teams will be tabulated and examined.

Background reading:

Bateson, P. P. G., 1966. The characteristics and context of imprinting. Biological Reviews, 41:177-220.

Eiserer, L. A. and H. S. Hoffman, 1974. Acquisition of behavioral control by the auditory features of an imprinting object. Animal Learning and Behavior, 2:275-277.

Gottlieb, G., 1971. Development of Species Identification in Birds. Univ. of Chicago Press, Chicago.

Hess, E. H., 1973. Imprinting. Van Nostrand Reinhold, New York.

Hoffman, H. S. and A. M. Ratner, 1973. A reinforcement model of imprinting: implications for socialization in monkeys and men. Psychological Review, 30:527-544.

b) Note to teachers

Day-old ducklings are a pleasure to work with; no student can be immune to their charms. This very simple exercise (which can also be done with other precocial birds but the results with Japanese quail are often not quite as neat as with ducklings) usually triggers a number of questions on communication (e.g., what is the parent's response to the distress call? what about siblings?) and on early experience in general. In fact, I often do this exercise in conjunction with another on imprinting such as that offered by P.H. Klopfer (in Price and Stokes, Animal Behavior in Laboratory and Field, 1975); birds left over from the imprinting exercise can be used in this one.

The persistency of day-old ducklings in following anyone moving is remarkable. If the followee also emits "come-come" calls, the bird falls all over itself as it races to the caller. To demonstrate the effects of the call alone, simply place callers in hidden positions at opposite ends of a room. If each calls alternately, the duckling invests a considerable amount of time and effort going back and forth across the room before it tires and emits distress calls.

B. Projects Developed by Chatauqua Participants

Many participants in past NSF-Chatauqua Biosociology short courses worked on interim projects during the 4 months or so between the first and second parts of the course. Some participants based their projects on ideas presented in the various handouts, while others generated entirely new projects appropriate to biosociological study. Since the participants represented a wide range of primary interests and background trainings, the projects reflected diverse approaches to the field.

I have selected a few of the projects for inclusion in the present working draft of this study guide in order to offer the reader a broader range of ideas for their own projects. In each case, the participant(s) who generated the projects have agreed to have their abstracts included and would welcome ideas and feedback from interested readers. The final version of this study guide will probably include an even more diverse group of project reports.

HORMONAL INFLUENCE ON COURTSHIP BEHAVIOR OF THE GUPPY, LEBISTES RETICULATUS

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The guppy is a very convenient organism to demonstrate hormonal effects on morphological and behavioral characteristics. The male initiates a series of behavioral patterns that are easily observed. The core sequence consists of following, luring, sigmoid curvature, display jump checking, and copulation. These display patterns plus male coloration can be developed in females by treatment with male hormones. A genetic female under the influence of male hormones will court untreated females employing the male courtship sequence. These results indicate the close relationship between behavioral patterns and internal hormonal conditions.

In order to demonstrate the effects of testostoerone on the development of secondary sexual characteristics and the courtship patterns of treated females, isolate immature females in a separate aquarium. The most effective method of exposure is to mix methyl testosterone in crystalline form with Tetra-Min dried fish food. The females should be fed the hormonally treated food at a dosage rate of 0.1 gm of methyl testosterone per day for one week and then 0.1 gm per week for an additional three weeks. This dosage level is for a five gallon aquarium. After approximately 30 days, full male coloration as well as elongation of the caudal and dorsal fin should be apparent. These characteristics should be retained for several weeks without apparent change.

Guppies can be used to demonstrate chain responses of courtship patterns. The untreated males and females will perform these patterns in a predictable fashion if kept isolated from each other 24 hours prior to the observation period. Students may be asked to identify particular behavior patterns of the male or female or both. After these patterns are established, an additional assignment could involve the sequence of these displays and the frequency with which they occur.

After a behavioral analysis of the untreated fish has been developed, the treated females can be exposed to the untreated females to establish the effect of hormones on sexual behavior. The behavioral sequence of the treated females should be essentially the same as the male pattern.

References

Baerends, C. P., R. Brouwer, and H. Tj. Waterbolk. Ethological Studies on Lebistes reticulatus. I. An Analysis of the Male Courtship Pattern. Behavior, 8:1955.

Bastock, Margaret. 1967. Courtship: An Ethological Study. Aldine Pub. Co. Chicago.

Clark, Eugenie and Lester R. Aronson. Sexual Behavior in the Guppy Lebistes reticulatus. Zoologica, 36:1, 1951.

Hildemann, W. H. Effects of Sex Hormones on the Secondary Sex Characteristics of Lebistes reticulatus. Journal of Experimental Zoology, 126:1, 1954.

VOCAL IDENTIFICATION IN EWE-LAMB BONDING

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Recognition and selective identification between mother and offspring is an obvious and basic social requirement for most species. The mother-offspring bond, which lies at the center of nurturance, protection, and socialization functions, originates and persists by virtue of communications which ensure accurate recognition. What is the nature of these communications? And what, if any, sequences or threshhold levels are involved in the communication-recognition process? Such questions prompted the exploratory investigation summarized here.

Our subjects were ewes and newborn lambs housed within the university's sheep barn. We first reasoned that the dam's recognition of her newborn would build and stabilize through a three-stage developmental sequence:

1. Olfaction (primary communication): Immediately after parturition, the ewe generally licks her newborn lamb(s) vigorously. This serves to warm and dry the lamb, to stimulate respiration and circulation, and to expose her to the apparently distinctive smell of her own offspring and birth fluids.

2. Vision (secondary communication): As the lamb literally moves further afield, recognition by sight supplants olfactory devices.

3. Vocalization (tertiary communication): Increased mobility and group mixing on the part of lambs decreases reliability of visual identification, with sound emerging as an essential supplement.

Our attention was thereby directed to determining (a) whether individual lambs do indeed possess a distinctive bleat, (b) whether the mother reacts to that bleat, and, if so, (c) at what age vocal recognition becomes operative.

Eleven lambs were selected, varying in age from a few hours to four days. Tape recordings of each lamb's cry were made, coded for our own identification, and subsequently played back at a pen enclosing the assembled ewes. We were unable to confidently identify any observable and relevant responses by the appropriate dams. We concluded that no responses had occured, noting in the process the difficulty of determining what constitutes "a response" -- a turn of the head?, an answering bleat?, gross bodily movement in the direction of the sound?

At this point in our explorations, renewed literature review reinforced a growing conviction that our attention had been focused, quite literally, in the wrong direction. We had noted in passing that, in enclosures containing a mix of several lambs and ewes, the lambs made very few sounds whatsoever, whereas there was frequent bleating from the adults. In adaptive,

functional terms, ewe-to-lamb communicational learning can, in fact, be seen as the more logical directionality. That is, the lamb's need for nurturance, protection, and shelter as provided by the mother suggests that identification abilities are the responsibility of the young, who must acquire auditory recognition skills as decreased physical proximity lessens the reliability of scent and visual cues.

Stage II of our investigation, accordingly, reversed our sender-receiver focus. Four ewes were separated from their offspring and moved to adjacent individual pens arranged in semi-circular configuration and blocked from view from the center area by a solid, four foot high wooden wall. Each of five lambs was carried in ("in hiding") and released within the open center area, free to select the pen of the appropriate mother in response to her omnipresent bleats if it chose to do so.

Our "true success" rate was 40%, meager on the surface but meaningful beneath. Two of the five lambs identified the correct ewe quickly and accurately. Two others demonstrated apparent efforts but did not locate successfully until further visual or tactile cues were provided. The remaining lamb showed a preference, but an inaccurate one. Table 1 displays the three success-failure differentiating characteristics that show some patterning.

Table 1. Summary of Results

	Successes		Failures		
Lamb	1	2	3	4	5
Sex	Male	Male	Female	Female	Female
Breed	Suffolk	Suffolk	Hampshire	Suffolk	Hampshire
Age	2 weeks	2 weeks	10 days	2 weeks	10 days

We suggest that age be given highest priority as an explanatory factor. It would appear that two weeks of age marks a threshhold level for the development of discriminating responses to auditory cues. Of our three "failures," only the two-week old showed any identificational interest that was both spontaneous and directed. We propose that this lamb's inaccurate choice may indicate the presence of individualized differences in localization ability, as distinct from a generalized perceptual ability.

As a concluding note, it is to be observed that commercial agriculture asks sheep, cattle, swine and poultry to perform economically under sets of environmental conditions quite alien from the environments in which their wild progenitors spent most of their evolutionary history. Study of the behavior of such domestic species and its application and utilization involves special problems and opportunities. For example, it is likely that one of the most important variables in experiments featuring observation, alteration, or manipulation of domestic animal behavior is the experimenter himself. We found in some of our subjects a tendency to orient towards us rather than towards the stimuli we were trying to present. Behavior of older animals is surely partly dependent upon their prior exposure to and experience with humans. Too often this earlier experience will be unknown and ignored, to the detriment of the basic knowledge and practical applications we seek through the fascinating study of animal behavior.

Reference

G. C. Anderson, "Old Wine in a New Skin, or Animal Behavior in the Modern Animal Science Curriculum," Journal of Animal Science 39 (1974): 441-46.

THE DEVELOPMENTAL ROLE OF TESTOSTERONE IN THE ONTOGENY OF INTERMALE AGGRESSION IN THE MOUSE

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Spontaneous aggression is largely sex and age dependent in most mammalian species. Castration prevents the display of intermale fighting, and testosterone replacement restores this behavior. In the study to be described, the quantitative relationship between circulating levels of androgen and aggressive behavior has been examined. In an attempt to simulate physiological conditions, silastic capsules containing several different doses of testosterone were implanted subcutaneously in male mice castrated at various stages of maturation. Radioimmunoassay was used to determine the developmental pattern of testosterone secretion and to monitor blood levels of testosterone in castrates administered exogenous hormone. Aggression was assessed in a neutral cage situation and olfactory bulbectomized males were used as standard stimulus animals. A test period consisted of three minutes during which time the latency to attack was recorded; a latency of 180 seconds was recorded if no attack occurred on a given trial. Stimulus animals were rotated in a round-robin fashion such that no two animals were paired together more than once.

Figure 1 illustrates the effect of castration on aggressive behavior in males castrated as adults and implanted with silastic capsules containing doses of testosterone that maintained blood levels of androgen equal to, higher than and lower than levels found in untreated males of the same age (as determined by measurement of accessory organ weights). Regardless of the dose of testosterone administered, only castrates implanted with oil showed a significant reduction in fighting following gonadectomy. The lowest dosage of testosterone used (a 0.3mg implant) was still sufficient to maintain aggressive behavior (8 of 10 animals fought); however, an approximately three-fold higher dose of testosterone was required to maintain normal weight of the sex accessory organs (intact male ventral prostate wt. = .42 $\pm$ .02 mg/g b.w.; 1mg implant animals' ventral prostate wt. = .42 $\pm$ .03). In fact, the low dose of testosterone (which maintained aggressive behavior) did not stimulate accessory organ growth as compared to castrated mice implanted with oil (0.3mg implant V.P. wt. = .19 $\pm$ .01; oil implant V. P. wt. = .21 $\pm$ .01).

Using these same doses of testosterone (10, 1, 0.3mg initial concentration), males castrated on the day of birth were studied following implantation of silastic capsules at 90 days of age. Males sham-castrated at birth served as a control group. Figure 2 illustrates the results of aggression testing. Only the 10mg implant induced fighting in gonadectomized males. The 0.3mg implant (which had maintained fighting in males castrated as adults) had no effect on aggression in neonatally castrated animals.

Figure 3 shows the results of aggression testing in males castrated prior to puberty. From radioimmunoassay results, a significant increase in circulating testosterone has been demostrated to coincide with puberty and the onset and display of intermale aggression. It can be seen from Figure 3 that the 1mg testosterone dose (which only partially induced aggression in males castrated at birth) was sufficient to induce fighting in males castrated at 25 days of age. However, while the 0.3mg implant maintained aggression in males castrated in adulthood, it also failed to induce aggression in males

castrated prior to puberty (puberty, defined as the onset of spermatogenesis, occurs around 35 days of age in the mouse).

The results of this study suggest that the physiological role of pubertal increases in blood testosterone is that of maximizing responsiveness of neural substrates for aggression to androgen encountered in adulthood. Androgen stimulation during perinatal life does not appear necessary for sensitization of neural substrates that mediate aggression, but the presence of circulating testosterone is required to maintain fighting in the adult male. In summary, ultimate sensitivity of the CNS to testosterone is dependent upon the amount and duration of previous exposure to androgen.

In another study using female mice ovariectomized as adults, it has been demonstrated that a 10mg dose of testosterone administered via silastic implants effectively induces spontaneous aggression, i.e., hyperphysiological blood levels of testosterone are sufficient to activate or sensitize neural substrates mediating "male-like" fighting behavior in adult female mice despite their lack of exposure to exogenous androgens during early life. This data is consistent with the hypothesis that adult sensitivity to circulating androgens is a sexually dimorphic phenomenon that is normally dependent upon previous exposure to androgen during development. Of interest is the finding that neural substrates mediating intermale aggression remain inherently bipotential in the adult mouse with respect to the capacity to respond to testosterone stimulation. The neural mechanism(s) whereby such bipotentiality is altered to a male-like state remain unclear.

FIGURE 1

Effect of Castration and Silastic Implants of Testosterone on Adult Male Aggression

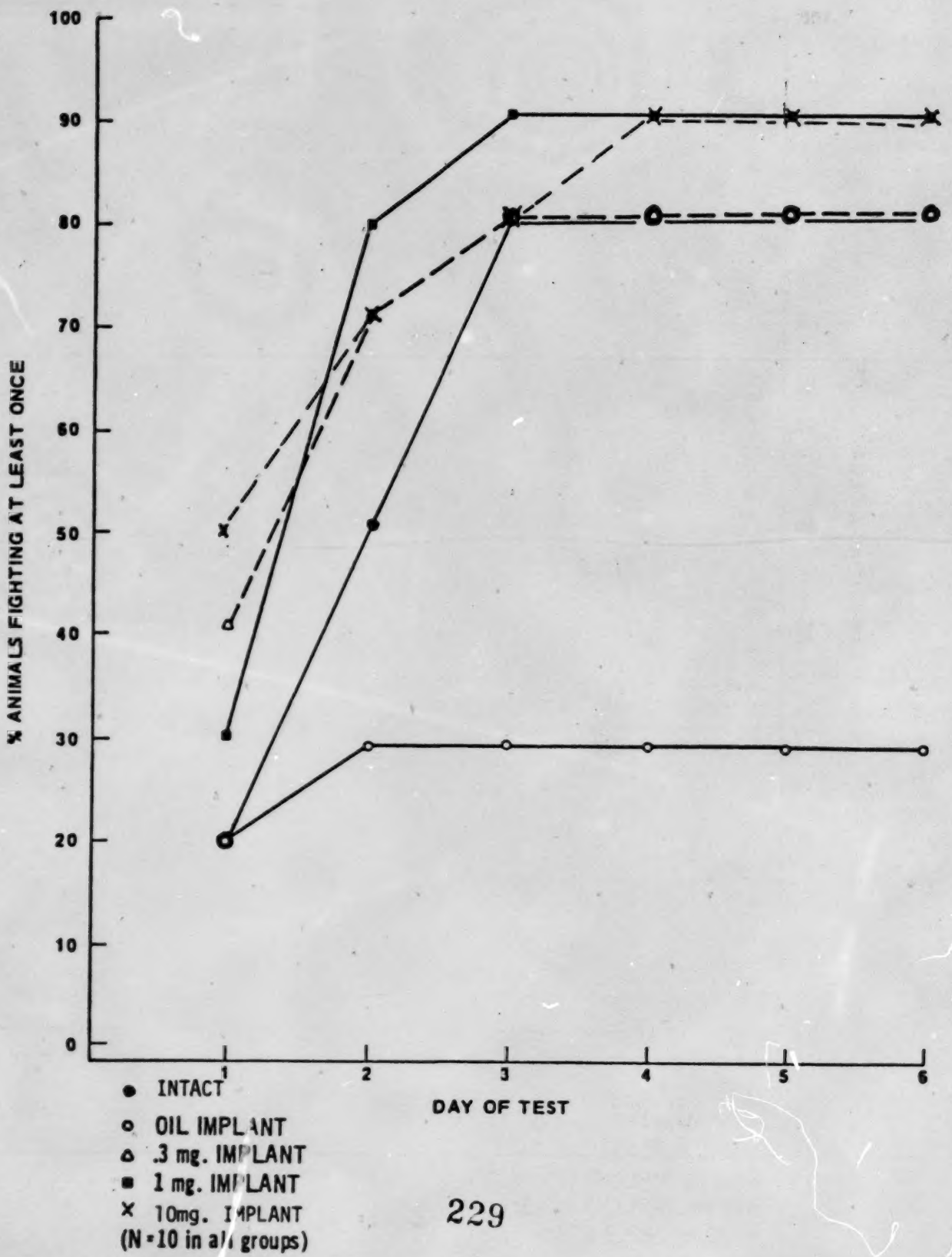


FIGURE 2

Effect of Neonatal Castration and Silastic Implants of Testosterone on Adult Male Aggression.

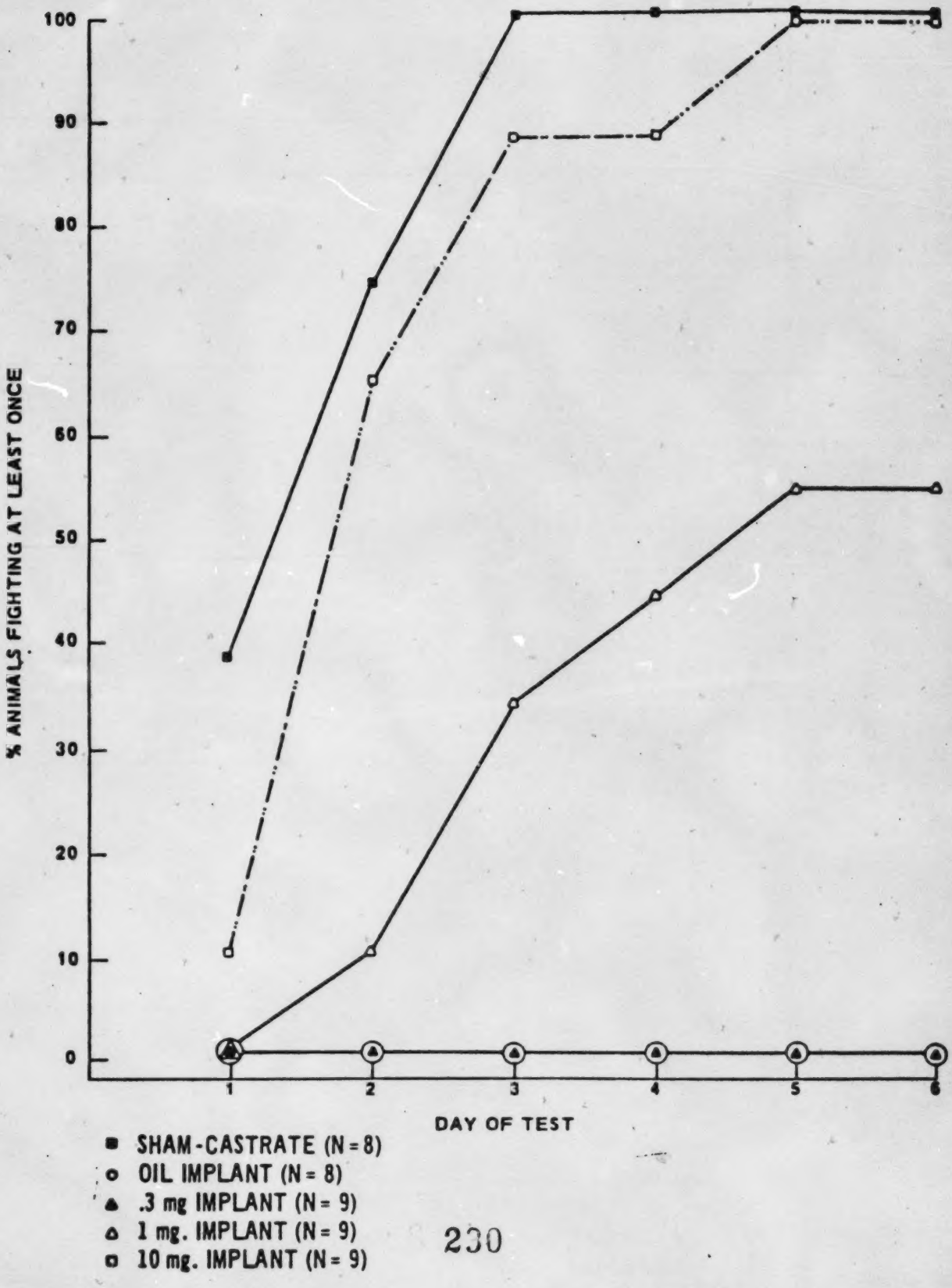
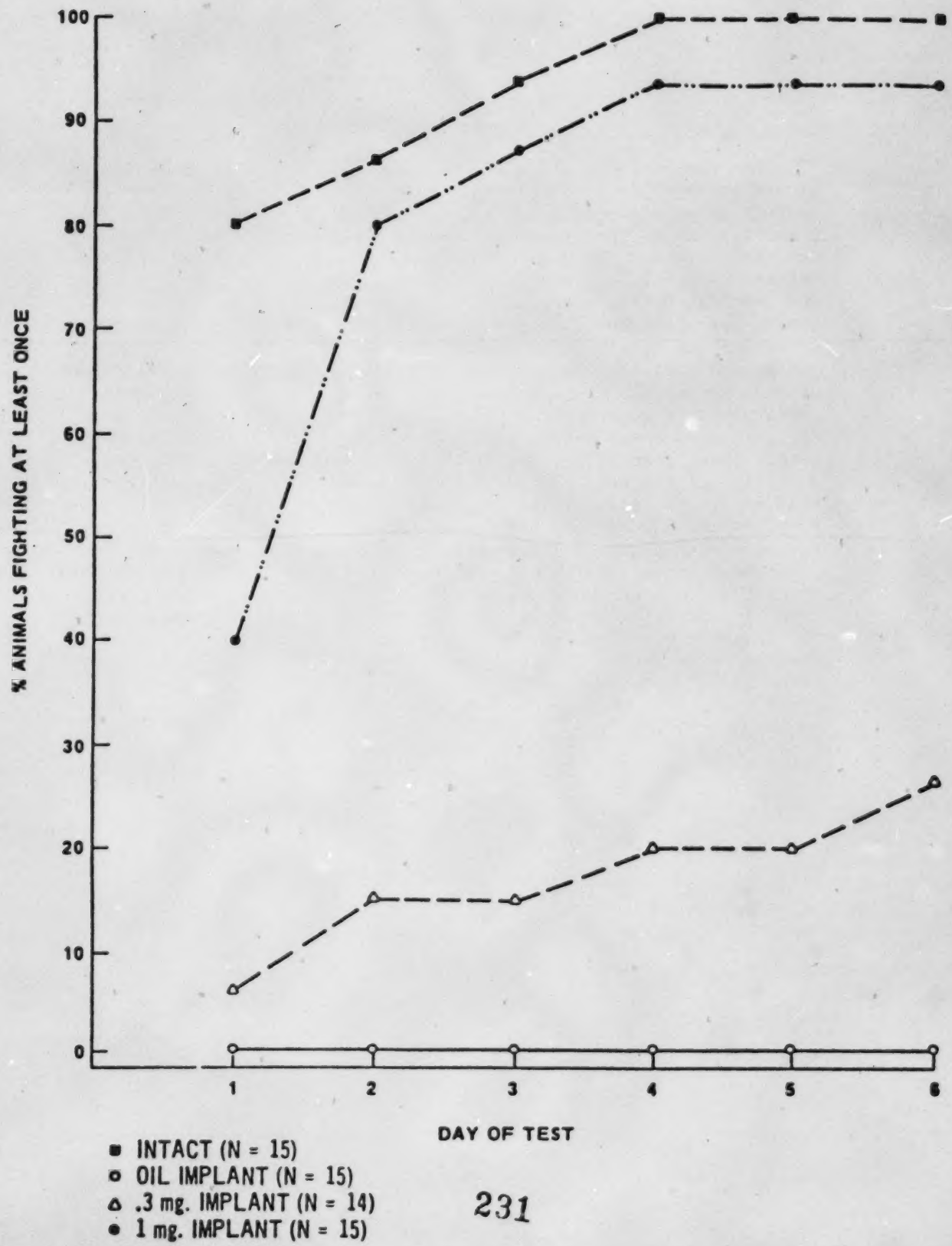


FIGURE 3

Effect of Prepubertal Castration on Adult Male Aggression



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AGGRESSION IN THE COLLEGE CLASSROOM: A PRELIMINARY ANALYSIS

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For the past two years the writer has been running a series of groups involved in an educational game called "The Cities Game". In this game political and social issues are presented to four power groups; Business, Government, Agitators and Slum Dwellers. Each of the groups begins the game with varying amounts of capital which is defined as power. On any given issue, each group decides its stand and negotiates with every other group to obtain the most favorable result for themselves. After the negotiation period each group votes and the result of the total vote either shows cooperation or dissension. Violence or aggressive benavior can be expressed in one of two ways; riots or unnecessary police action. There are only three possible vote totals that can lead to one of these two possible aggressive outcomes out of a total of 32 possible alternative vote totals (less than 10%). One might expect that over the long run, about 10% of the vote totals should be aggressive in nature (riot or unnecessary police action). This was not to be however. Out of 46 total issues 24, or over 54% turned out to be aggressive in nature, far more than a chance difference, statistically.* The writer concludes tentatively (although much more work needs to be done in this area) that this may be a specific measureable effect of the socialization of aggression into our youth in the sense that competitiveness is stressed in our society as a necessary condition to succeed in our larger society and in its smaller representative, the educational classroom.

*Z of 10.14 p. less than .001

DOMINANCE IN MAN

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At various times people can be seen to interact in a manner that suggests competition for dominance to be taking place. This exercise attempts to stage such a situation so students may observe the means whereby individuals attempt to promote and maintain dominance over one another.

Procedure:

1. Ask for three or four volunteers who have had some experience in camping. These individuals are told that each must select from a list of equipment the seven most important items for survival on a three month canoe trip in a wilderness. The volunteers must then provide the class one list through common agreement.

2. The volunteers are asked to step into the hall and not to communicate with one another while the class is informed of which items are recommended by experts.

3. When the volunteers have gone, the class is told that the actual purpose of the exercise is to observe the interaction of the volunteers as they attempt to create a common list of items from their separate lists. The class is told to observe such behaviors as body carriage, volume of voice, "certainty" of vocal expression, facial expressions, gestures, and any other means whereby the volunteers attempt to impose their opinion upon the group.

4. A list of equipment is placed on the blackboard including such items as canoe, paddles, canoe repair kit, rope, axe, fish hooks, matches, a book entitled "How to Survive in the Wilderness", etc.

5. The volunteers are brought in one at a time and each is asked to pick seven items from the list. Someone records the list of each.

6. When the list of each volunteer is finished these lists are placed on the board and the volunteers are asked to assume a position in front of the class and to create a common list of seven items.

7. Upon completion of the common list (you may find it necessary to terminate discussion by the volunteers before they are finished) the volunteers are told the true nature of the laboratory exercise and classroom discussion takes place on

the interaction that all have observed. Discussion could cover the following:

a. What were the common means of "persuasion"?
b. Was dominance or a dominance hierarchy observed?
c. How could these behaviors be quantified?
d. What similarities and differences exist between the dominance interaction of our species and those of other species?

Problems you may encounter:

1. The most troublesome difficulty has been to place the volunteers before the class in such a manner that their interaction can be seen and heard by the class. They frequently go into a huddle.

2. A sticky problem is encountered when class discussion of the volunteers begins. Our society places a premium on aggressiveness and dominance (maybe all societies do) and I always worry that a submissive volunteer may have hurt feelings from a tactless evaluation by a peer. This problem can be avoided to some extent by a judicious selection of volunteers.

3. The class will have great difficulty describing some aspects of the interactions they observed. Such things as body carriage and facial expression can be very subtle, but they are real and play an important role in communication. This problem can't be solved, but you can turn it to your advantage by letting it demonstrate one of the major difficulties in the study of animal behavior; namely, how to define and describe the units of behavior.

Suggested Readings

Darwin, C. 1872. The Expression of the Emotions in Man and Animals. London: (Chapters 8 and 14 especially).

Morris, D. 1967. The Naked Ape. Dell Publishing Co. New York, N.Y. (The chapter on Fighting).

STABILITY OF SEATING ARRANGEMENTS IN A FREE CHOICE SITUATION

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Hypothesis: Given a free choice, students will select a location for sitting on the first class day and will remain in that position throughout the quarter.*

The study setting: At the beginning of the winter quarter 1973-74 a study of the daily seating patterns was begun in 3 classes of Biology at Enterprise State Junior College. No seats were assigned, all students were free to sit anywhere at any class period. All classes were held in the laboratory with 16 tables, 32 stools and 3 desks. The length of the study was 10 weeks.

Group A: 21 students started quarter; 18 completed the quarter.
Group B: 35 students started the quarter; 30 completed the quarter.
Group C: 16 students started the quarter, 16 completed the quarter.

Results:

Group A (meeting time, 8 A.M.). The 21 students in the class selected seats on the first day. No mention was made by the instructor of seating but note was made of the seating pattern as roll was called. During the quarter 3 students were lost from the course, but no adjustments were made in the seating of the remaining students. Stools were moved by the instructor during the course of the study: once the stools were moved to another room and many times small shifts were made in the class room. In every case, students returned the stools to the original positions.

Group B (meeting time, 9 A.M.). The class was very crowded since the lab is designed for 25, not 35, students. Again students made a free selection of seating and note was taken on the initial role call. During the quarter 4 students withdrew and one student simply quit coming but there was no change in actual seating arrangement. The only student seating adjustments made were those allowing a bit more room. During the course of the 10 weeks, stools were moved many times to random places in the lab and into other rooms. In every case the stool was returned by the student to the original position.

*Ed. Note: The phenomenon of self-imposed stable seating arrangements has been observed in our classes for a number of years and has formed the basis of several student projects in our behavior courses. To our knowledge, the phenomenon (and its various ramifications in human ethology) has never been fully examined.
M.W.S.

Because of the overcrowded room the examinations were administered in a much larger room. The student could sit anywhere that he or she chose. With 125 seating places available, the 31-35 students aligned themselves in a pattern almost identical to that seen in the regular class room. They were farther apart, but in the same basic pattern.

Group C (meeting time, 11 A.M.). The smallest class had no withdrawals. Students seated themselves at random. (In this group were 7 students who had been in previous classes in the same room, this being their 3rd or 4th class. In all cases but 2 they seated themselves in the same place in the class room as in previous classes.) Each student remained in the same position for 6 weeks. In the 6th week one student, male, shifted to an empty seat directly behind his first selection. After several days in the new position the instructor mentioned the shift and told the class of the study. The next day every student in the class had shifted widely from the original selection. The instructor made no mention of the moves until class was almost over, then said "It will be interesting to see how long you last." The next day every student was seated in the original selection, except the one male who was in his second choice. When questioned about the return to original seating the students said that they did not feel comfortable in the new position.

Conclusion

The hypothesis was well validated by the study: only 1 student out of 72, over a 10 week period of time, moved from the original selection. Absences, tardiness, stool moving, room changing and the like did not significantly effect the students' original selection of seating positions in any of the three classes. It was also noted that students who have had previous classes in the same classroom tended to sit in the same position quarter after quarter, and that examination scores and grades did not reflect any relationship to seating patterns.

IS IT REALLY THAT CROWDED HERE? A STUDY IN PERSONAL SPACE

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Problem

The research done was a study of the behavior of the species Homo sapiens, variety university undergraduate. The study was made at the University of Puget Sound, Tacoma, Washington, in January and February, 1975. The problem was the investigation of human behavior within the context of biosociology, with a view to the comparison of the responses of both human and nonhuman animals to crowding.

Method

The study began with a brief survey of writing in the fields of animal and human behavior on the following subjects: (1) the comparative study of animal and human behavior, (2) territoriality, (3) space requirements, (4) crowding, (5) responses to crowded conditions. For animal behavior the chief sources consulted were works by W. C. Allee, John B. Calhoun, and John Paul Scott; for human behavior the principal sources were the writing of the anthropologist Edward T. Hall and the psychologist Robert Sommer.

The survey of the literature was followed by a field study on the subject of personal space.[1] The method used was, first, the compilation and distribution of a questionnaire on space available to students and their use of it in a men's and women's dormitory and, second, analysis of the questionnaire results in terms of space requirements, crowding, and responses to crowding.

Assumptions underlying the study were: (1) students live in nearly intolerably crowded conditions. (This assumption is based on numerous students' statements over a period of five or six years and is supported by my impressions[2] during visits to students' dormitory rooms.); (2) what with national economic conditions and the plight of private universities at the time of study, the situation is likely to get worse before it gets better.

The questionnaire was open-ended and dealt with the following general topics:

1. Demography (age, sex, class in school, how long in dormitory).

2. Type of dormitory accommodations (room or rooms, number sharing, how dormitory space used).

3. Personal space history (size of family and family home, type of personal space before coming to university, sharing of space).

4. Reactions to dormitory conditions (evaluation of space needs for sleep, study, storage, recreation; judgment of suitability of accommodations).

5. Comparison of personal space at home and in dormitory (amount, suitability).

6. Housing plans for the following academic year.

Results

The findings of the field study were inconclusive in that (1) the 35 students who completed the questionnaire could not be considered a representative sample of the undergraduate population and that (2) in the light of the study's basic assumptions, the students' responses showed a considerably greater satisfaction with dormitory space available to them than other students' statements had led the researcher to expect. (Of course, the basic assumptions may have been wrong.)

The majority (60 per cent) of the respondents were freshmen, as compared to a small minority (14 per cent) of upperclassmen. (UPS, unlike many universities, does not have a large freshman class in proportion to the size of the sophomore, junior, and senior classes.) An even larger majority (71 per cent) of the respondents were males, a situation that is not true of the student body as a whole. Here one may infer that in a study of this type sampling is particularly important.

In order to find whether or not their home experience had predisposed them for or against the crowding that is unavoidable in most university dormitories, students were asked to compare the space available to them in their homes and in the dormitory. Sixty-six per cent said they had more room at home. Eighty-three per cent of the total reported that they had their own room at home, as compared with the average number of students per dormitory room (based on the responses of 33 out of the 35 students) of 2.3.

In response to the question of whether they had enough space in the dormitory to live comfortably in their preferred style, 46 per cent said that they did, 49 per cent, that they did not. When asked if they had enough of various types of space available to them, students gave the following positive responses:

Type of space	Per cent
Sleep	86
Study	63
Recreation	48
Storage	40

Concerning their housing plans for the next academic year, 40 per cent of the students were planning to move, either to other dormitories or off campus. Here I might comment that it is a common practice for UPS students to live on campus for their first year or two and then move off campus in search of more space and greater privacy and freedom in their activities. (The University policy concerning both student housing and the rules and hours for their movements is quite permissive.) The tendency toward movement away from campus housing after the freshman year would suggest that a significant number were not satisfied with their accommodations.

Interpretation

It is my impression that UPS students value dormitory life during their freshman year, for it helps them get started in an orderly routine without the necessity for exploration and individual problem-solving when they are having many new experiences. Also, they value the opportunities to meet new friends in their residences. However, as they establish friendships and become accustomed to the university routine, the disadvantages of crowding and a high noise level become more important to them, and many tend to move off campus. This may well be a commentary on the function of the dormitory in introducing students to university life.

As for comparisons between human and nonhuman animal behavior, I am sure that the concepts of territoriality and space requirements are relevant to both. However, beyond this I have questions. As a social scientist I do not feel competent to judge distinctions between various types of social animals and thus am hesitant about making generalizations from the needs and behavior of animals to those of humans. For example, is Calhoun's well-documented concept of the behavioral sink really applicable to humans? Humans have, at least in theory, resources that animals do not: migration based on an understanding of their circumstances, building upward in crowded cities, the ability to understand, predict, warn against--and possibly to forestall--harmful events. Here also the dimension of cultural variation gives humans in dense populations the expectation of crowding and very possibly a greater tolerance for it than people in sparser populations having different cultural traditions.

Here questions of taxonomy arise. Certainly much of the taxonomic history of genus Homo is arbitrary, if not fanciful. From the standpoint of behavior, are cultural variations among different human groups perhaps analogous to variations between species or subspecies of animals? How much do we dare generalize between animal and human behavior without a thorough knowledge of both?

Postscript

The study of personal space is being used as background for a proposed study of privacy in the campus life of university students. Using the concepts of territoriality and personal space, it is proposed that in the fall term of 1975-76 at the University of Puget Sound students in the course The Individual in Society, an introduction to Comparative Sociology (anthropology and sociology combined), will make a study of the privacy needs of fellow-students living in campus and off-campus housing. It is proposed that the students will be divided into teams each of which will study a different type of housing (men's, women's, coed dormitories; fraternities and sororities; and various off-campus accommodations), using questionnaires and interviews, in order to determine existing conditions and possible answers to students' needs for privacy.

Notes

1. Personal space is defined as "an area with invisible boundaries surrounding a person's body into which intruders may not come," and likened to "a snail shell, a soap bubble, an aura, and 'breathing room.'" Robert Sommer, Personal Space: The Behavioral Basis of Design. Englewood Cliff, N.J.: Prentice-Hall, Inc., 1969, p. 26.

2. An interesting observation, triggered by a question asked by a participant in the Biosociology course at the time the study results were presented, was that although many students seemed to be critical of the accommodations available to them, none had in my experience used crowding or lack of privacy as a rationale for unsatisfactory academic performance.